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THE SYSTEMATICS OF FOSSIL AND RECENT SALAMANDERS
(AMPHIBIA: CAUDATA), WITH SPECIAL REFERENCE TO
THE VERTEBRAL COLUMN AND TRUNK MUSCULATURE

by



BRUCE G. NAYLOR

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Chapter III

PRINCIPLES OF SYSTEMATICS

A. Morphology and Phylogeny

i) Phylogenetic reconstruction

Various attempts, both explicit and implicit, have been made to define principles of phylogenetic reconstruction. At one time, characters having little or no adaptive significance were believed to be especially useful in phylogenetic study. Writing of the *Amphibia*, Noble (1931, p. 90) concluded with respect to patterns of "dentition, pupil form, pectoral girdle, [and] tongue form," that "many of these parallel changes have no known functional significance." As he used these as important diagnostic features, it seems these "characters of *Amphibia* [that] have no functional significance" (Noble 1931, p. 93) were considered good taxonomic characters. Darwin (1859), however, recognized long before that, by and large, the most important taxonomic characters are of significant "physiological" (= functional) import (see also Cain 1959b). The characters used by Noble in his classifications are certainly important, but precisely because they are functionally crucial.

Numericists would argue that there should be no selection or weighting of characters (see Sneath and Sokal 1973), but that all (or as many as practicable) features of organisms should be used in the determination of relationships. As noted below (also Hull 1970), this philosophy is both impossible to implement and undesirable as an ideal.

Some characters prove more significant (and more useful) than others in reconstructing phylogeny and in the production of a classification. Nevertheless, in less extreme form, the claim that reconstruction of phylogeny should be based on many characters is true.

Cladistic systematists insist on using only shared-derived (or apomorphic, see Hennig 1966) characters. For example, although not explicitly cladists, Wake and Özeti (1969, pp. 124-125) state that "information concerning relationship in primary groups (e.g., the family Salamandridae) is contained only in derived character states. Resemblance that results from characters shared in states that are primitive for the primary group has no phylogenetic information." In a restricted sense this claim is true (and recognized well before the advent of cladism). However, it is not true to claim that characters presumed to be primitive hold no phylogenetic information. What such characters lack is cladistic information, the confusion resulting from usage of phylogenetic as an improper synonym for cladistic. Phylogeny includes two different, but linked, components: cladistic and plesiomorphic. Perhaps to emphasize the distinction, rather than writing of "phylogenetically" (read cladistically) significant characters, one should use characters of evolutionary significance. Evolution subsumes phylogeny, which subsumes cladistic relationships, but not vice versa. Common retention of presumed primitive features indicates similar evolutionary history, owing to conformity of genotype and selective regimes. All characters, whether interpreted as relatively primitive (plesiomorphic) or relatively derived (apomorphic), hold a certain amount of evolutionary, and hence phylogenetic, information.

The argument against exclusive use of presumed apomorphic features becomes stronger upon rejection of cladistic assumptions and acceptance of the concept of the morphocline (see Maslin 1952, and below). That is, rejecting the (subjective) assertion that only cladistic relationships should be of interest, one necessarily rejects the claim that primitive characters are valueless. Reaching this point, it is necessary to consider principles of phylogenetic reconstruction.

Hennig (1966) discussed the criteria to be used in the determination of the polarity of a transformation series (or morphocline), suggesting the following:

1. Geological character precedence (biostratigraphic criteria).
2. Chorological progression: advanced characters tend to be found in those species that have departed furthest geographically and/or ecologically from the initial ancestor.
3. Ontogenetic precedence (ontogeny recapitulates phylogeny).
4. Correlation of series of transformations.

In addition, Hennig (1966) explicitly recognized that reversals, convergence, and parallelism would cause difficulties in utilization of these criteria. His suggestions are, by and large, valid, but are sometimes ignored by some who claim to be his followers.

I suggest the following as criteria to be used in the determination of morphocline polarity, and thus of phylogeny:

1. That character state found in the earlier fossil representatives of a higher taxon should tend to be the more primitive. This is based on the theory of evolution by natural selection as applied to the sampling of true phylogeny by the fossil record. It is (or should be)

obvious that an actual evolutionary sequence must have the ancestral characters occurring prior to the more derived. Earlier fossil species, therefore, tend to approximate more closely to the ancestral state and are judged to be primitive. As recognized by Hennig (1966), paleontology often provides clues as to actual ancestral states. Only paleontological data are truly historical, allowing one to infer actual time dimensions (Simpson 1961).

One of the more powerful arguments for the inclusion of biostratigraphic data in the determination of ancestor-descendant and sister-group relationships is that, in geology, the concepts work. Dating and correlation of fossiliferous rock sequences have been exhaustively tested throughout investigations since the time of William Smith (see Wood et al. 1941, on correlation of the North American Tertiary by means of fossil mammals). The system has been critically used and not falsified. In addition, as noted, the fact of descent with modification stands in powerful support of the use of biostratigraphic data in phylogenetic investigations (for a contrary view, see Schaeffer et al. 1972).

Geological criteria are most important in groups possessed of an adequate fossil record (e.g., early reptiles and amphibians, see Romer 1966 and references therein; horses, see Simpson 1951) and it is evident that urodeles lack an adequate record. The known fossil species belong to several different families, and are scattered temporally and geographically. Owing to this sporadic record, it is not possible to place similar specimens in any sort of morphological sequence (perhaps excepting the Batrachosauroididae, see below).

It is also evident that the more derived, neotenic species have been disproportionately sampled in the Mesozoic and early Cenozoic. The fossil record may be used to the extent of documentation of first known occurrences so as to aid inferences about minimum times and areas of origin. Nevertheless, in study of the interfamilial relationships within the Caudata the living species must form the basis for a system into which the fossil taxa may be fitted. Although with salamanders this is the only possible approach, it is not to be taken as advocating a devaluation of the fossil record.

2. That character state found in a higher taxon that is, on independent evidence, determined to be relatively plesiomorphic should tend to be primitive. This is Hennig's (1966) correlation of transformation series, and basically derives from Cuvier's "Law" of the Correlation of parts. The entire organism is the unit of selection (Mayr 1963), each structural unit or complex being acted on in the context of relationship to and interaction with other such units within the animal. As noted by Cuvier, for example, ungulates tend to have high-crowned, grinding teeth and hoofs, in addition to other correlated features. In spite of the celebrated exception of chalicotheres, the "law" is true as an observational generalization. While recognizing mosaic evolution to be a very real phenomenon, this criterion can be used as an aid in the elucidation of morphocline polarity.

3. A character state shared by members of one taxon with members of a related taxon will tend to be primitive (for at least one of the taxa), especially when the character state is located at the ends of

the two morphoclines. This is the principle of ex-group comparison. For the Caudata, comparison with anurans, caecilians, and fossil amphibians may indicate the relative primitiveness of certain character states. For example, anurans generally have external fertilization, as do two of the living families of urodeles. This feature is also shared with "lower" vertebrates (fish), and is likely to be primitive for the Caudata. In the same way it may be said that paired pre-maxillae with short nasal spines are probably the ancestral state, retained in hynobiids and cryptobranchids.

The criterion may also be used within the Caudata: for example, the structure of the trunk musculature and vertebrae in the Ambystomatidae. Based on correlations of transformation series, general structure, and ontogenetic evidence, the trunk musculature and vertebrae of hynobiids are probably the most primitive of living salamanders. This accepted, the close resemblances of *Ambystoma macrodactylum*, *A. maculatum*, and their allies to hynobiids in this character complex, and the divergent, foetal condition of *A. tigrinum* and its allies cast serious doubt on Tihen's (1958) determinations of the primitive vertebral state for ambystomatids (see below). The same argument applies to the frontosquamosal arch, which is almost certainly derived within the Salamandridae.

4. Data from studies of different ontogenetic states. Developmental stages from larva through to metamorphosed adult can provide valuable information for use in phylogenetic investigations. This is especially true of salamanders, which have utilized paedomorphosis (evolution via neoteny and paedogenesis) to a large degree. The Caudata are excellent examples of the concepts of de Beer (1958) and of the

rejection of "recapitulation" as a general law. Features that appear primitive on first view are often shown to be derived owing to paedomorphosis. In the Caudata, the simple is often the apomorphic, in spite of what intuition might indicate, as is shown by the structure of the skull and trunk musculature. On the other hand, it has been assumed that complex lateral abdominal musculature is the more primitive (e.g., Noble 1931). Nevertheless, it is more likely, upon considerations of larval patterns, that the possession of many layers of abdominal musculature is a derived, foetal condition. Ontogenetic evidence was also used by Wake (1966) in his elucidation of the primitive and derived states of the premaxilla in plethodontids, and has been necessary in the proper interpretation of the family Ambystomatidae (see below).

It is to be emphasized that none of these criteria are infallible. All possible data must be considered in order to arrive at reasonable conclusions. Maslin's (1952) suggested criteria can also, depending on circumstances, be used as clues in phylogenetic reconstruction, but caution is necessary. He (1952, p. 69) assumed that "morphoclines are partially or entirely identical to the chronoclines from which they are derived." Although this could well be true in any given case, it might just as easily be false. I know of no empirical or reasonable theoretical considerations that would tend to support this as a valid generalization. Each population travels a unique evolutionary path, changing as directed by selection so as to maintain adaptation. There is no known mechanism that might cause primitive organisms to remain so, unless this is adaptive (see Brundin 1972a for a different, although vitalistic, view).

Maslin (p. 56) also believed that "convergence is relatively rare." Study of the fossil record (e.g., early bony fishes, early reptiles, and mammal-like reptiles) and of living populations (e.g., the *subvertebralis* of newts and certain plethodontines) documents the weakness of this assumption. A tremendous amount of parallelism and convergence has been recognized and much must go unseen. Hennig (1966) noted that these phenomena must be carefully considered in phylogenetic research.

To work, Maslin's criteria and those suggested above must be augmented with detailed studies of the transformations within the morphoclines. That is, functional relationships and environmental correlations (see Cain 1959b) must, in so far as possible, be studied and the most probable sequences determined. Moreschachi (1973) notes the necessity of deciding what known structures could have served as ancestral states. In this way, ancestral states may be inferred from features believed to be primitive.

In spite of such cautions, I suggest that Maslin's criteria are basically reasonable and useful. The main criticism is, perhaps, of the possibility that strict utilization of them would make phylogenetic analysis rigid. Nature is multiform and complex, making it necessary that operating principles be broad and flexible, with the organisms rather than the rules providing the ultimate guide. Principles are generalizations and not necessarily completely true; one must be ready to discard them whenever they are contradicted by nature.

I take the position that "good" phylogenetic characters have the following features:

1. They are part of a coherent adaptive complex, the functional significance of which is more or less understood.
2. They can be studied in a series of lower taxa and the differences and functional reasons for the differences can be studied by means of morphoclinal analysis.
3. They are useful for ex-group as well as in-group comparisons.
4. They are preservable in fossil specimens, so as to allow direct comparison of past and present.

Darwin (1859) discussed "good" characters in classification, a treatment that still has importance today. He (1859, p. 415) stated that "almost all naturalists lay the greatest stress [in classifying] on resemblances in organs of high vital or physiological [i.e., functional] importance," but "the mere physiological importance of an organ does not determine its classificatory value." Darwin (p. 417) noted that "a classification founded on any single character, however important that may be, has always failed; for no part of the organism is universally constant." The usefulness "of trifling characters, mainly depends on their being correlated with several other characters of more or less importance" (Darwin 1859, p. 417). In these quotations, substitution of "phylogenetic reconstruction" for "classification" shows the importance of Darwin's ideas to present-day phylogenetic analysis.

In many cases the adaptational significance of a given character is obscure or unknown, and this has been a problem in the present study.

Nevertheless, when differences in character states can be related to changes in adaptive strategies and environment, it is easier to interpret morphoclines. If this approach is taken, the phylogenetic information in the characters increases and phylogenetic reconstruction becomes more meaningful (Cain 1959b). Upon acceptance of the fact that structures usually exist for precise functional reasons, this is the only logical approach.

Functionally important character complexes have been, in practice, accorded heavy weight in phylogenetic studies (Darwin 1859). Feeding and locomotory systems are important in the study of the relationships of fishes (Greenwood et al. 1973), and have been among the more extensively used in the systematics of salamanders (Noble 1931, Regal 1966, Wake and Özeti 1969). Such systems are clearly important to the continued survival of lineages, and it is often possible to determine functional reasons for the differences between taxa. This allows characters to be weighted more validly.

In investigating the interfamilial relationships of the Caudata (or in any other such study), it is necessary to consider each family in detail. It is not sufficient to choose one or two representatives from each family and then hope to develop realistic hypotheses of relationship between families. First, intrafamilial morphoclines must be clearly known. Once morphocline polarities within families are decided, comparisons can be made between families. In my study, the new data come mainly from the trunk musculature and vertebrae. As many genera as possible from each family were dissected, allowing for comparison of vertebral structure and correlated patterns of the

myomeres within families. Each familial morphocline may then be compared with those of other families in order to match end points and determine polarities. In some cases (e.g., sirenids and amphiumids) familial "morphoclines" necessarily consist of a single character state. Once interpreted, the morphoclines allow theoretical judgements as to probable phylogenetic sequences.

Utilization of the morphocline allows flexibility and extensive use of in-group and ex-group comparisons. Judgements can be made as to what state could, in theory, most readily have given rise to other states, both within and between families. Furthermore, the congruence, or lack thereof, between morphoclines of different characters is more apparent. The flexibility of this approach should be regarded as a virtue, but perhaps its lack of rigidity deprives it of the qualities of a panacea, contributing to its lack of use.

It is essential that characters be useful for ex-group comparisons. Characters having only one state within a family and that are not derivable from a particular state in another family have little value in the determination of either intra- or interfamilial relationships. It is necessary that characters vary from taxon to taxon and that, if possible, they also vary within taxa. For example, as the nasolabial groove is unique to the Plethodontidae, derivable from no known structural ancestor, and does not vary significantly within the family, it is quite useless as a character on which to base any phylogenetic theory. This was overlooked in Edwards' (1976) phylogenetic treatment of the Caudata, in which the nasolabial groove is purported to have some (unstated) sort of significance.

A more definite example from the Caudata may be illustrative. The *subvertebralis* shows marked structural diversity within this order, with most of the families having a more or less unique and readily distinguishable configuration of the myomeres. In addition, the Ambystomatidae, Plethodontidae, and Salamandridae each show an intra-familial morphocline of this unit and, together, a single interfamilial cline (see Fig. 90 and above descriptions). In ambystomatids the morphocline may be considered to show only a single state, although this is an oversimplification. As indicated by comparison with the Hynobiidae, ambystomatids have the primitive (phenetically and probably ancestrally) sort of well-developed anterior basapophyseal muscles and associated flexures. Plethodontids display a distinct morphocline running from the primitive condition in *Plethodon*, with the posterior flexures shifted medially and the anterior basapophyseal muscles suppressed; through *Eurycea*, with distinct development of neomorphic posterior basapophyseal muscles; to *Pseudotriton* and the desmognathines, with progressive increase of the posterior basapophyseal muscles. In addition, a secondary morphocline includes species of *Plethodon*, *Batrachoseps*, and certain bolitoglossines: all trace of the subvertebral flexures is lost, converging upon the salamandrid newts. In the Salamandridae there is a single, simple morphocline including *Salamandra* at the more primitive end retaining posterior flexures and the newts, with loss of these flexures.

Accepting that the *subvertebralis* of hynobiids and ambystomatids exhibits the primitive condition, it is possible to compare and interpret the morphoclines. The basic trend is from complex to simple, a

common situation in the Caudata. The plethodontid morphocline may be joined to that of the ambystomatids, with *Plethodon* representing the more primitive end of the cline. Similarly, the salamandrid cline joins to the plethodontid, with *Salamandra* exhibiting the primitive structure. The resulting scheme to some extent mirrors what I understand to be the phylogenetic history of the three families, but it is to be stressed that this joining of familial morphoclines of a single structural complex does not produce a phylogeny, although it is a reflection of it. Evidence from other systems must also be considered and structural complexes that are functionally linked with the *subvertebralis* must be interpreted, such as the nature of the inter-central joint, epaxial myomeres, lateral abdominal musculature, and the general configuration of the vertebrae. When the different morphoclines have been analyzed and compared, contradictions may be resolved, judgements made, and hypotheses of relationship proposed.

Finally, in consideration of morphoclines it must be remembered that ancestors existed in the past. At best, contemporaneous species can only provide structural approximations to true ancestral states. Whereas it is perfectly acceptable to derive plethodontids from an ambystomatid-like ancestor, which (if known) would be properly classified in the Ambystomatidae, it is not meaningful to derive living plethodontids from living ambystomatids. By contrast, in the case of plethodontids and salamandrids, data from other systems (e.g., vomerine teeth, lunglessness, and structure of the middle ear) tend to contradict the derivation of the latter from a plethodontid ancestor. Rather, descent of the two families from a common ancestor (probably

most similar overall to plethodontids) seems the most reasonable interpretation.

Owing to the historical nature of phylogeny, it is helpful if characters used in studying living organisms be applicable to fossil specimens, so that past and present are more directly comparable. With respect to salamanders, trunk musculature provides such a complex of characters. In many cases, the sort of trunk musculature is directly reflected in the structure of the trunk vertebrae. Thus, fossil vertebrae having posterior or anterior basapophyses (for example) are readily interpretable in terms of extant salamanders (see below). Similarly, cranial osteology, spinal nerve exits, and ossified hyobranchial elements can often be used in both fossil and Recent taxa. By contrast, phylogenetic reconstructions based exclusively on patterns of courtship, karyology, or structure of the ear are not useful with respect to fossil specimens.

ii) Karyology

Study of the number and structure of chromosomes and of the amounts of nuclear DNA in different species provides information potentially of use in phylogenetic study (see Chiarelli and Capanna 1973, Moreschalchi 1970, 1973, 1975). However, the relative importance of karyological evidence as opposed to data from other aspects of the phenotype is not clear. As karyological data have been used as important components in phylogenetic reconstructions of the Caudata, it is necessary that they be considered. The karyotype is an important aspect of the phenotype, but must be studied and interpreted in the same way as any other feature (see also Moreschalchi 1973).

One must be cautious about any single character used to construct a phylogeny (Darwin 1859). It has been argued that karyotypes have "a lower adaptive value as compared to other morphological features . . . [and] for this reason, karyotype [sic] variations reflect general phyletic lines" (Benazzi 1973, p. 5). The adaptive nature of the karyotype may be debated, but it is probable that this part of the phenotype is constructed in just as adaptive a fashion as any other (Cain 1964, Nikolsky 1976). Enthusiasm for karyology is another attempt to use little understood (or "non-adaptive") features as important taxonomic characters, even though such usage is not valid (see Darwin 1859, pp. 414-417, Cain 1964).

Environmental correlations in the context of the theory of natural selection can provide suggestive, although tentative, evidence of adaptation for any character. For example, large amounts of DNA and large cells in dipnoans and paedogenic salamanders correlate with freshwater environments subject to changes in temperature, salt concentrations, and ionic balances. Metabolism is slow in relation to necessary adjustments to environmental flux (see Szarski 1970, 1976). These correlations indicate the probable presence of adaptation. Goin et al. (1968) noted a correlation between smaller amounts of DNA in amphibians and more rapid progress through larval stages. Papers by Olmo (1973), Olmo and Morescalchi (1975), and Morescalchi (1973, 1975) contain information on the adaptive nature of the amphibian karyotype. Nikolsky (1976) provides a more general model to account for variations in chromosomal number in fish.

Morescalchi (1973, p. 238) noted that "the cytotaxonomic study of the higher families [of amphibians] is found to be immediately useful only at very general levels." However, "the integration of these [karyological] data with anatomical or other types of data . . . may always prove useful indications for a precise definition of the evolutionary [sic] lines followed by these vertebrates." The same may be said for any structural feature. In order to determine the primitive chromosomal situation in the Amphibia, Morescalchi (1973) used two criteria:

1. A model common to the more "generalized" forms of the three orders.
2. A karyotype that could have given rise to a second, but from which it could not be as readily derived.

These lead to the same model: a karyotype with a high number of chromosomes, many acrocentric chromosomes, and many microchromosomes. Morescalchi (1973) interprets the Cryptobranchoidea as primitive, with asymmetrical, bimodal chromosomes; those families with asymmetrical, unimodal chromosomes as intermediate (Sirenidae and Proteidae); and those with symmetrical chromosomes as most derived (Amphiumidae, Ambystomatidae, Plethodontidae, and Salamandridae). Except for the position of sirenids and proteids, which I believe to be owing to secondary reversion (see below), Morescalchi's reconstruction (1973, fig. 14) is quite similar to mine.

Karyology can contribute to evolutionary studies, but such evidence must be treated cautiously. There does seem to have been an overall trend to reduce chromosomal number within the Caudata,

but the reasons for this are unknown and it does not appear to have been universal. The sirenids are perhaps tetraploid (Morescalchi 1975, Morescalchi and Olmo 1974). Cryptobranchids are all but certainly derived with respect to hynobiids, yet the living species of *Cryptobranchus* have higher numbers of chromosomes than do hynobiids. In the structure of the trunk, proteids are derivable only from an opisthocoelous ancestor. In spite of a relatively high chromosomal number ($2n=38$), they cannot be directly derived from hynobiids. In such cases gross anatomy takes precedence over karyology.

In more or less paedogenic, permanently aquatic salamanders (Amphiumidae, Proteidae, Sirenidae, and Cryptobranchidae) there has been an increase in the amount of cellular DNA (Morescalchi 1975, table II). This gain can only be interpreted as convergent in these groups and appears to be of a purely adaptive nature (compare dipnoans). In spite of the apparent lack of overall close correlation between phylogeny and karyotype throughout the Caudata, there are correlations on lower levels. Karyology certainly provides clues to phylogenetic understanding, but it is surely more profitable to investigate adaptation than to "reconstruct" questionable or nontestable phylogenies based on single (even though ill-understood) characters.

iii) Concepts and Cautions

Comparative anatomy and homology.— Zangerl (1948) advocated a clear separation in morphology of factual results (gained from observation and comparison) from the interpretation of these results. His criticism of the trend towards not publishing the data (descriptions and

comparisons) in favour of reporting only the interpretations is well taken. Theories hopefully conform to observations, and to report only the former is not scientific. In this regard, an historical perspective is helpful: the timeless works are those filled with good factual observations. As science evolves, theories may change, but the descriptions and observations remain useful. The most revolutionary and influential contribution to biology, *On the Origin* (Darwin 1859), owed its original (and hopefully continuing) theoretical impact to the detailed facts marshalled to support the theory of evolution by natural selection.

In spite of this agreement, acceptance of Zangerl's (1948) argument for a divorce of data collection from interpretation is not possible. As noted by Darwin (1859), data collection cannot possibly take place in the absence of theory. "I can have no doubt that speculative men, with a curb on, make for the best observers" (C. Darwin, in Darwin and Seward 1903, II, p. 133). It is neither possible nor profitable to attempt observations untouched by theory and then, subsequently, decide what they might mean. The problems with Baconian research have been discussed by Hull (1970, 1974) and Ghiselin (1969), among others.

Zangerl (1948, p. 354) states that "morphological concepts are factual generalizations from observed structural relationships and as such *they do not and cannot carry phylogenetic implications*" (italics original). He argues that phylogenetic inquiry lies outside the area of morphology, which is not to be harmed by theorizing. Given the present evolutionary framework of biology, I do not believe that this

position is tenable. Rather, morphological concepts of necessity carry phylogenetic implications. In studies such as mine, morphology serves as a tool to elucidate the relationships of the families of urodeles, among other things. Theory and observation must, therefore, proceed hand in hand in a relationship of reciprocal illumination (Hennig 1966).

Even in "pure" comparative anatomy concepts are important. Those features that are compared must be homologous in the evolutionary or phylogenetic sense. Given that evolution (descent with modification) has occurred, we *define* homology as based on derivation from common ancestry. Homology is a definition, not a theory. Whether two structures are homologous is another question. Structures are homologous if one hypothesizes that they have been derived from a feature possessed by an ancestor common to the taxa being compared. Phylogenetic conclusions are drawn by observing and comparing structures in different taxa to decide whether they are homologous. A conclusion that structures are homologous is also a conclusion as to the genealogical relationships of the organisms possessing the structures, but this is not circular. The definition of homology may be circular, but as definitions are tautological such a comment is not profound. The critical question is whether the application of the concept of homology is circular. This, of course, does not have to be the case.

Primitiveness.— The concepts of phenetic and ancestral primitiveness are important in phylogenetic analysis, and the two are not necessarily synonymous. Phenetic primitiveness is used, for example, in groups of contemporaneous organisms when it is stated that taxon (or character) A

is plesiomorphic with respect to taxon (or character) B. This means that, given present information, one taxon can in principle be derived from the structural conditions of another. In phylogenetic study it is hoped that phenetic primitiveness approximates to ancestral primitiveness and that structural ancestors reflect real ancestors. However, whether or not taxon (or character) A is truly ancestral is another matter. Ancestral primitiveness is used when it is stated that taxon A *is* ancestral to taxon B. In such cases the fossil record is, of necessity, involved because the taxon hypothesized to be ancestral must have preceded the descendant.

As soon as a lineage splits, or when one gives rise to a second, the two lineages are subject to continuous selection in the context of differing genotypes and environments. There is, therefore, no reason to argue that a plesiomorphic taxon necessarily preserves partially or entirely the structural conditions of the true ancestor. Such may be so, but that is to be determined on the merits of the individual case and with the deciding criteria coming, if possible, from the fossil record.

Parsimony.— The concept of parsimony is often used in science and is frequently resorted to when two opposing theories are compared. It is held that, in absence of other information to be used in testing, the choice between two otherwise equally plausible hypotheses is to be made on the basis of the principle of parsimony. An hypothesis is to be constructed with a minimum number of supporting assumptions, the reason being that simpler hypotheses are more readily testable. With fewer supporting theories (assumptions) it is easier to test the major

theory itself. Otherwise, any test or observation that might seem to falsify a theory could be owing simply to the invalidity of one or more of the supporting assumptions, rather than to problems with the major theory. Parsimony does not derive from the assumption that nature is simple, but from the methodology of science (see Popper 1968a,b).

Parsimony may be misused in support of special interests. For example, it should not be claimed that the more parsimonious phylogenetic reconstruction is necessarily the one with the fewest number of branching points. "The fact that one bases a method of phylogenetic interpretation on parsimony does not require that evolution be a parsimonious process, although many researchers believe it is" (Hecht and Edwards 1976, p. 672). Simple cladograms may well be, at base, extremely unparisimonious. That is, the assumptions necessary to support a simple (or simplistic) phylogenetic reconstruction may well be numerous. A simple phylogeny with numerous assumptions would then be less parsimonious than a phylogenetic reconstruction with more branching points but fewer supporting assumptions.

Embryology.— Although data from ontogeny can be extremely useful, especially with salamanders, the biogenetic "law" of Haeckel is here explicitly rejected. In spite of attempted restoration, the concept has been so effectively negated (de Beer 1958, Ewer 1960) as to need little discussion. Ontogenetic information is as important as that from any other area, but it is no more important and cannot be used to substitute for good fossil evidence. The use of recapitulation necessitates adherence to evolution by means of gerontomorphosis, that is, of phylogenetically new adult stages being added (see de Beer

1958, pp. 36-37). As documented by de Beer (1958) and almost ideally confirmed by salamanders, however, paedomorphosis (evolution by accentuation of larval stages) has been a much more common occurrence. Furthermore, when the embryo is properly viewed as an adapted system providing for the most efficient production of the adult stage, the "law" that ontogeny recapitulates phylogeny is clearly false.

Numerical analysis.— As a general rule, it may be said that the problem in phylogenetic research is not inability to handle large amounts of information, but an inability to order the data theoretically and reasonably. Numerical methods are often invaluable tools, but they cannot substitute for theoretical and interpretive input (see Hull 1970, Ghiselin 1969, p. 21). Characters are to be chosen for informational content and applicability (see above), not because they are simply available and readily measured and coded.

In attempts to develop more "rigorous" classifications and phylogenetic reconstructions, workers have turned to cluster analysis of many characters. Krogh and Tanner (1972) argue for the extensive use of computer techniques in systematic work, but their study of the Ambystomatidae suffers from problems that computer analysis cannot remove. As they point out, the hyobranchium and its associated musculature provides all of their characters. Therefore, although 48 factors were used in analysis (Krogh and Tanner 1972, pp. 59-61), the outcome is still a single character phylogeny. The hyobranchium is an integrated, although complex, system composed of intricately related structures (see Larsen and Guthrie 1975, Lombard and Wake 1976, 1977). Treating such a system as a large number of component parts

("characters"), although useful for functional analysis, is more likely to be misleading than enlightening in a phylogenetic study. Further, although a valuable contribution to comparative anatomy, the work of Krogh and Tanner (1972) suffers from lack of theoretical interpretation. Before cluster analysis can be used to elucidate phylogeny, characters must be weighted by judgements as to presumed primitive and derived states, structural sequences, and functional *raison d'être*.

In their study of intergeneric relationships within the Salamandridae, Wake and Özeti (1969) made interpretations of primitive and derived states, thus partially analyzing the data prior to cluster analysis, and used characters from more than one adaptive complex. Characters judged as primitive were rejected as having no phylogenetic information, however, and owing to misinterpretation in several cases (see below) and the misuse of correlations of character states, analysis was partially biased. Character states for which judgement as to primitiveness was not possible were assumed to be primitive (or derived) if they happened to correlate with another character believed to be primitive (or derived). Owing to misinterpretation of the nature of the frontosquamosal arch (see below), several linked misidentifications followed. Finally, the phenomenon of convergence was ignored in the case of *Salamandrina* (probably owing to over-utilization of characters from the hyobranchium), and ex-group comparisons with other families, which are essential in determination of morphocline polarity, were not possible owing to lack of information. These criticisms do not devalue the contribution of Wake and Özeti (1969), whose descriptions are important, but show the need for caution in numerical analysis of data.

Edwards' phylogenetic reconstruction.- Finally in this section on cautions, the most recent phylogenetic analysis of the Caudata must be considered. Edwards (1976) proposed a new classification and phylogeny of salamanders. The study purports to be based on several characters, but the phylogenetic information present in many of these is low or nonexistent. His phylogeny and the classification that follows from it are ultimately double character systems, based on chromosomal number and the pattern of spinal nerve exits. These two characters are certainly important (and his proposals are close to mine), but other data are ignored.

Edwards (1976, pp. 318-321) uses the following characters:

1. *Presence or absence of the angular bone.* This serves only to distinguish the Cryptobranchoidea.
2. *Internal or external fertilization.* Again this serves only to distinguish cryptobranchoids (and questionably sirenids) from other salamanders. The information provided by Salthe (1967) is not utilized.
3. *Patterns of replacement of vomerine teeth.* These patterns are not compared across familial lines (see Regal 1966) and there is no analysis of morphoclines.
4. *Chromosomal number.* This is useful for interfamilial interpretations.
5. *Pattern of exits of spinal nerves.* This is also useful across interfamilial lines.
6. *Number of gill slits.* This feature tells little or nothing of phylogenetic relationships of the families, the numbers are not compared across familial lines, and there is no interpretation provided (see also Hecht and Edwards 1976).

7. *Presence or absence of the second epibranchial in the adult.*

This is a loss character (see Hecht and Edwards 1976) serving only to distinguish cryptobranchoids and, perhaps, sirenids.

8. *Free or fused columella.*

The treatment of this character is oversimplified. There is in fact a wealth of phylogenetic information contained in the auditory apparatus (Kingsbury and Reed 1909, Reed 1920, Monath 1965), which is ignored in this study, leading to misleading results.

9. *Presence or absence of the lacrimal bone.*

"The complete loss of a character state does not indicate evolutionary direction or relationship, nor does it indicate whether the distribution among taxa is the result of parallel or convergent evolution. It is impossible to determine whether the loss of the character occurred independently or was the result of directional selection. All relationships based on loss of shared and derived characters have zero state information and must be seriously questioned" (Hecht and Edwards 1976, p. 655).

10. *Presence or absence of the ypsiloid cartilage.*

This feature is not useful in interfamilial interpretation of salamanders as there has been demonstrable independent loss in various lineages (see also Hecht and Edwards 1976, p. 655).

11. *Presence or absence of maxillary bone.*

This is another character having no informational content for interfamilial relationships. It is a loss character and also correlates with paedomorphosis (see also Hecht and Edwards 1976).

12. *Presence of the nasolabial groove.*

This feature has no informational content at the interfamilial level, as it is unique to

plethodontids and lacks structural antecedents in other families.

"The apomorphous features characteristic for a particular monophyletic group (present only in it) can be ignored in discussing its relationships to other groups" (Hennig 1966, p. 90).

There is a tendency for all workers to make sole, or major, use of certain characters (either those with which one is working or that tend to support a certain theory) in phylogenetic analysis and to ignore or explicitly reject others. Characters or morphoclines that tend to controvert one's phylogenetic models must be discussed, however, and it is necessary to explain why contradicting facts are considered to be of less importance than the supporting evidence. In their recent consideration of the relationships of the Proteidae, Hecht and Edwards (1976) discuss 18 characters used by previous workers to demonstrate monophyly for the family. Their detailed treatment of evidence in conflict with their hypothesis of polyphyly is admirable, allowing one to readily see areas of disagreement and to clearly follow the arguments. In this sense, my disagreement with their conclusions (see below) is incidental.

As recognized by Darwin (1859), divergence and extinction are real phenomena, creating the gaps observed between living taxa. This being so, reconstruction of phylogeny of Recent animals in the absence of paleontological data is especially difficult, unless clear and reasonable principles are used. These criteria must be consistent with evolutionary theory and with information from organisms that have a good fossil record (i.e., mammals). Principles derived from organisms

lacking such a record (that is, for which information as to what really happened is absent) are necessarily likely to be less realistic, especially when they conflict with information from phylogenies that are reasonably certain. The caudate amphibians present the situation, seen also in fish and insects, of abundant living representatives and a poor fossil record. There is, as yet, no possibility of utilizing the fossil record to test the conclusions reached by previous workers and in this study. Therefore, my work must be tested on its own merits as to whether it is parsimonious, internally consistent, and in agreement with presently known data. The suggested relationships are testable hypotheses (or predictions) as to what should be expected in future studies if they are true. Hopefully those studies will include paleontological research.

B. Biological Classification

i) Introduction

Competent biologists accept that the concept of evolution best explains our observations of the organic world. Darwinism is therefore the theoretical basis of biological inquiry, including the discipline of taxonomy. This being so, biological classification should reflect our understanding of the evolutionary history of organisms. It is probable that, perhaps excepting some pheneticists, all systematists would agree with this thesis, but how best to express evolutionary relationship remains an area of contention.

As in politics, taxonomic theorists are divided into three camps — pheneticists (Sneath and Sokal 1973), evolutionists (Darwin 1859,

Mayr 1969, 1974, Simpson 1945, 1961), and cladists (Brundin 1966, 1972a, Hennig 1966). Unfortunately, the debate has also become political, with emotion substituting for reason and dogma for argument. Nevertheless, an optimal method should exist for ordering the organic world. I argue that this method is the evolutionary one, as its pragmatic and theoretical bases are the most firmly tied to Darwinism and selectionist theory.

Phenetic taxonomy will be only briefly discussed, as there have been excellent critiques of the methodological and philosophical problems inherent in that system (Hull 1967, 1968, 1970, Johnson 1970). Sneath and Sokal (1973) continue the more extreme phenetic approach, but largely ignore the criticism directed at their theories of classification. The most devastating discussion of computer taxonomy (Hull 1970) is not mentioned or cited in their recent text.

Gillispie (1960, p. 261) notes that "the theory of natural selection is what turned the study of all living nature into an objective science," yet numericists advocate a taxonomy divorced from evolutionary concepts. Sneath and Sokal (1973, p. 18) even reject the fundamental ideas of the biological species and phylogenetic homology, desiring "to redefine them or possibly even dispense with them." Numericism can be viewed as an attempted retrogression to pure Baconian philosophy — the belief that facts must, in some way, be collected "objectively" and theory then developed subsequently. This philosophy has never been applied in science (Kuhn 1970) and facts can only have significance (indeed, can only be seen as facts) in relation to some theory.

Hull (1970) stressed the impossibility of separating classification from theory — even pheneticists have theories. Any scientific research must proceed hand-in-hand with theoretical considerations. "Purely phenetic classifications . . . are impossible and . . . even if they were possible, they would be undesirable The idea that an extensive and elaborate classification can be constructed in isolation from all scientific theories and then be transformed only later into a theoretically significant classification is purely illusory" (Hull 1970, p. 32).

Pheneticists (e.g., Cain 1959a, Gilmore 1951) assert that, as the largest source of error in classification is reliance on theory, one must classify neutrally. "Such a procedure would assuredly be safe, but in the extreme it is impossible . . . and in moderation undesirable" (Hull 1970, p. 34). Once again, an attempted rejection of theory in classification is met, but as Kuhn (1970, p. 79) notes, "there is no such thing as research in the absence of any paradigm [= theory]. To reject one paradigm without simultaneously substituting another is to reject science itself."

Pheneticists (Sneath and Sokal 1973 and references therein) claim that a classification must be "useful" — their criteria of usefulness being content of phenetic similarity and information retrieval. However, "classifications . . . are incapable of storing much in the way of specific information. Rather than being storage-and-retrieval systems themselves, they serve as indexes to such storage-and-retrieval systems. The information resides in the monograph" (Hull 1970, p. 28). Further, that a classification should be useful is misleading. The ends

of taxonomy "are better characterized by the words *theoretical significance* than by *usefulness*. An extremely accurate scientific theory of great scope will certainly be useful, but there are many things which are useful, though of little theoretical significance" (Hull 1970, p. 50, italics original). This is not to negate numerical methods as valued tools in the construction of classification, but to reject the discipline as a theoretical framework for classifying real organisms.

ii) Principles of Biological Classification

Although it is not possible to axiomatize biological classification in the sense of Popper (1968a,b), a list of premises or principles may be suggested. The major premise is that Darwinian evolution has occurred and that classification must therefore be consistent with the inferred evolutionary history of organisms. Granting this premise, the following are suggested as the principles upon which a biological classification is to be based:

1. Categories are to be collective, uniting related organisms (monotypic taxa are to be avoided).
2. The taxonomic hierarchy is to reflect both cladistic and patristic relationships, that is, should reflect evolution (see Darwin 1859).
3. Fossil and Recent species are to be classified in one system.
4. Ancestral species existed in the past and have been sampled by the fossil record, and as such are as real and discoverable as are sister-group relationships. The existence of ancestral taxa is to be reflected in classification.

5. Taxa are to be monophyletic *or* paraphyletic at the lowest *possible* level.
6. All characters carry evolutionary, and thus taxonomic, information of differing import.
7. Phylogenetic reconstruction and classification are complementary, not synonymous.
8. Ranking of taxa is arbitrary, but not to be based on *a priori* assumptions.

The major premise is composed of two parts, the first of which can find no disagreement amongst informed biologists. The second part would, perhaps, be unacceptable to some cladists and pheneticists. The objections of the latter have been noted and those of the former are discussed below. The eight principles are not ranked in any order of importance, as their relative contributions to evolutionary taxonomy are indefinable, but linked.

The first principle, that categories are to be collective, seems well established. Mayr (1969, p. 236) observed that "the taxonomist must make every effort to keep the number of monotypic taxa as low as possible. Slightly aberrant species should whenever possible be included in the same genus as the most nearly related species." Simpson (1945, p. 231) notes "the vital fact that bringing things together is the more useful and important function of taxonomy." There is little disagreement over this concept in the taxonomic literature, with one cladist (Crowson 1970, p. 54) even suggesting a drastic lumping of genera in order that "it might become practicable to memorize all the valid generic names in quite extensive groups."

The advantages of this suggestion are doubtful, but excepting certain cases (such as the first known bird, *Archaeopteryx*) monotypic taxa are to be avoided.

The second principle follows from the premise that classification should reflect evolutionary relationships. The ways of inferring these relationships are discussed above. The phenetic school states that such relationships can be ignored *or* that they are best discovered by phenetic analysis (Sneath and Sokal 1973), whereas cladists assert that only cladistic relationships are relevant for classification. Evolutionists believe that both cladistic and patristic relationships must be used in classification (see Darwin 1859, Hull 1970, Mayr 1974, Simpson 1961).

Evolutionary theory is the paradigm under which biologists should work. This being so, classification must be consistent with our understanding of the evolutionary history of the group under study. There are two components to this history: splitting of lineages *and* structural change of lineages (Darwin's descent with modification). Neither phenetic nor cladistic analysis alone can hope to elucidate the course of evolution. Splitting of lineages is seemingly controlled by geographic isolation (on whatever level) of populations and/or natural selection (Mayr 1963). However, changes in lineages are controlled, not during or by splitting (contra Brundin 1972a,b, Eldredge and Gould 1972), but by natural selection acting within the framework of the species' genotype and the environment at every point in time. There is little observational or theoretical evidence that cladogenesis is directly linked or causal to the process of

modification by natural selection. The phenomena of cladogenesis and divergence are separate, although both are governed ultimately by natural selection (Gingerich 1974, Mayr 1963, Williams 1966). To concentrate on one to the exclusion of the other is to violate evolutionary theory and to impose a false simplicity on nature.

The third principle states that fossil and Recent organisms are to be classified together. This principle needs little defence as all schools appear to accept it (Hennig 1966, Simpson 1961, Sneath and Sokal 1973, but see Patterson and Rosen 1977). Crowson (1970, p. 67) advocates "a separate classification for each era of the geological past," but this would produce an unworkable system, suited mainly to obscuring evolutionary relationships.

The fourth principle contends that ancestral species existed, that they are real and discoverable in the fossil record, and that they must be utilized in a system of classification. It has been recognized that, in order for Hennigian classification to stand, this principle must be rejected. Therefore, Nelson (1973, p. 311) has "assumed that ancestral species cannot be identified as such in the fossil record [as] . . . this assumption is fundamental to Hennig's phylogenetic systematics." It is stressed that ancestor-descendant relationships are hypothetical (Nelson 1970), but of course sister-group relationships are no less hypothetical and one should not reject either system of relationship. Rather, each situation must be judged on its own basis, using the information at hand. In some cases an hypothesis of descent from a common ancestor will be most reasonable, in others one of an ancestor-descendant relationship will be

preferred. In the sense of parsimonious and realistic (that is, scientific) hypotheses, objections that ancestor-descendant relationships cannot be proved are trivial in that science does not concern itself with proof (see Popper 1968a,b). Although imperfectly, the evolutionary approach can incorporate ancestor-descendant relationships into a classification (as well as into phylogenetic analysis), the cladistic system cannot.

It might even be disputed, theories of classification aside, whether cladistic analysis is to be preferred in all cases. Certainly when considering only Recent organisms, cladistic methods are excellent, as they do not (explicitly) attempt to force contemporaneous species into roles of ancestors and descendants. For clarity of expression, cladograms are used when applicable in my phylogenetic analysis below. However, if the fossil record is considered, it becomes unreasonable to limit oneself to analysis separated from stratigraphic data and inferred ancestor-descendant relationships, forcing all organisms into a single time plane.

Figure 91 is redrawn from Schaeffer, Hecht, and Eldredge (1972, fig. 1). It is claimed (Schaeffer et al. 1972, pp. 40-41) that "a cladogram [Fig. 91A] claims less than, but actually says as much as, a phylogenetic tree" and that "a phylogeny . . . is a theory of relationships expressed in the form: Taxa A and B are more closely related to each other than either is to C." However, neither of these assertions can be accepted. Firstly, comparison of Figure 91A and 91B makes it evident that both diagram the same theory of relationships, with no real ancestors recognized in either case. Both "claim" the

same thing, but the phylogenetic tree in Figure 91B "says" a good deal more than that in Figure 91A, as the former shows known stratigraphic ranges. Comparing Figures 91A and 91C, it can be seen that the latter both "claims" more and "says" more than the cladogram. In some cases it is more reasonable to hypothesize direct ancestor-descendant relationships, and to claim less than is warranted is not scientific. Secondly, based on evolutionary theory, phylogeny is real and it is certainly not a statement of two taxa being more closely related than either is to a third. Such a statement expresses an hypothetical cladistic relationship, which hopefully conforms to some real phylogeny. Even an hypothesis of phylogenetic relationship is, in some cases, more than a statement of inferred sister-group relationships. Ancestors are real and if the evidence supports an hypothesis of ancestor-descendant relationship it is unreasonable to claim less. Whenever nature fails to conform to a model, it is not nature that is to be changed.

It is accepted by cladists and evolutionists that taxa should, ideally, be monophyletic (principle 5), although certain pheneticists have advocated that this be ignored. Sneath and Sokal (1973) attempt to have things both ways, stating that "phenetic groups are usually monophyletic" (p. 47), but elsewhere that classifying a taxon with the group with which it converges rather than with the group from which it originated "is more generally useful" (p. 57). Even in phenetic terms, the "usefulness" of such a procedure is doubtful.

A point of contention remains, however, between cladists and evolutionists. Cladists argue that a taxon must be strictly

monophyletic, that is "a group of species descended from a single ("stem") species" (Hennig 1966, p. 73). If actual stem species could be recognized by cladistic taxonomists, they would have to be classified separately, with a rank equal to that of the two derived taxa (Nelson 1973). According to Hennig's definition, taxa such as the Osteichthyes, Amphibia, and Reptilia are invalid as they do not include all species descended from their (hypothetical) common ancestor. In his terms they are paraphyletic.

In evolutionary taxonomy, the criteria for monophyly are less rigid. Although the aim is to produce taxa that are monophyletic at the lowest practical level, Simpson's definition is usually followed. This states that "*monophyly is the derivation of a taxon through one or more lineages . . . and from one immediately ancestral taxon of the same or lower rank*" (Simpson 1961, p. 124, italics original). Paraphyletic taxa cause no concern, in recognition of the fact that there are patristic components to phylogeny (see Darwin 1859) and that the adaptive zone of a taxon is an important evolutionary phenomenon (see also Van Valen 1971), worthy of expression in classification.

Evolutionary systematists recognize that monophyly at a low level is desirable, and this is reflected in their classifications. Nevertheless, empirical evidence and selectionist theory admit the possibility (or probability) of several lineages giving rise to a higher taxon in such a way as to be indistinguishable. "It seems more reasonable to assume that several to many phyletic lines are involved in the origin of new groups This pattern is not in conflict with any positive paleontological data, and it is in close agreement with the concepts

of mosaic evolution and transitional adaptive zones, and with the diversification shown by recent groups of organisms" (Bock 1965, p. 280). Nelson's (1970, p. 383) claim that his earlier (1969) classification of the vertebrates is made up of taxa that "are, or at least seem to be, monophyletic in the strict sense of the word, i.e., at the level of the biological species" is merely an untestable hope (and most probably false).

The contention that all characters hold evolutionary, and hence taxonomic, information of one sort or another (principle 6) will find support amongst pheneticists and evolutionists, but disagreement from cladists. It is a cladistic axiom (Hennig 1966) that only apomorphic (shared-derived) characters can be used to determine relationships. In the strictest genealogical sense this is, perhaps, true, although cladists were not the first to use the principle of shared and derived characters in phylogenetic analysis. Further, plesiomorphic is a relative term (see below) and as evolutionary biologists our concern should be with all the relationships and attributes of organisms.

In Figure 92 is diagrammed a scheme of relationships between seven Recent taxa. Taxa A, B, and G are each accorded familial rank (actually the families Amphiumidae, Ambystomatidae, and Cryptobranchidae, respectively). The taxa C, D, E, and F each represent a genus (of the Hynobiidae). Block 1 represents a complex of characters hypothesized to have been present in the ancestral urodele stock and therefore plesiomorphic with respect to the taxa under discussion (although not necessarily to the Amphibia). Block 2 is a complex of characters uniting taxa C, D, E and F and believed to approximate to the characters

of block 1. Therefore, if C, D, E, and F are to be united in a common family, this can only be done on the basis of characters plesiomorphic to the Caudata. Block 3 is an apomorphic complex of characters separating taxa A and B from the other taxa.

It is not known from which taxon (C, D, E, or F) that the derived groups A+B and G arose, only that they originated from taxon C+D+E+F (the Hynobiidae). Therefore, in Figure 92, the positions of C, D, E, and F are completely interchangeable. Following strict Hennigian principles, each of taxa C, D, E, and F would have to be separated into a taxon of rank equal to that of A+B (Ambystomatoidea) and G (Cryptobranchidae). However, the retention of a plesiomorphic complex of characters in the central group does indicate a common ancestry and similar selective pressures. The practicality and theoretical significance of separating each of the hynobiid genera into its own family is not intuitively obvious. It would neither reflect the evolutionary history of the group nor, given present understanding, elucidate cladistic relationships. Whether a character state is plesiomorphic or apomorphic differs according to in-group and ex-group comparisons. For example, the attainment of the nasolabial groove and lunglessness in the plethodontids is apomorphic with respect to the Caudata, but plesiomorphic when only plethodontid taxa are considered. Primitive characters have also been discussed above in the section on Phylogenetic Reconstruction.

The assertion that phylogenetic reconstruction (see above) and classification are complementary, not synonymous, processes is contentious (principle 7). Phylogenetic reconstruction and cladistic

analysis attempt to infer the branching of species and higher taxa. For such studies, Hennig's (1966) principles are in many cases very useful. Classification, however, orders known species in a hierarchical system for the purposes of indexing and cataloguing, making use of inferred phylogenies and phenetic gaps. It serves as an indexed system for general reference, not in the generation of hypotheses. Real organisms and inferred phylogenies are heuristic, leading to further testable hypotheses. A list of names organized in a classification does not, in practice, serve any heuristic function.

"I believe that the *arrangement* of the groups within each class, in due subordination and relation to other groups, must be strictly genealogical in order to be natural; but that the *amount* of difference in the several branches or groups, though allied in the same degree in blood to their common progenitor, may differ greatly, being due to the different degrees of modification which they have undergone; and this is expressed by the forms being ranked under different genera, families, sections, or orders" (Darwin 1859, p. 404). The theoretical significance and practical application of a classification that exactly duplicates a cladistic reconstruction have not been satisfactorily explained. Such a system is highly unstable, changing by necessity each time different cladistic relationships are hypothesized. In an evolutionary classification, concepts of phylogenetic events can often change rather markedly, yet leave the classification untouched. Owing to the labelling and cataloguing functions of a classification, stability is most desirable, making the evolutionary system again preferable to the cladistic.

The final principle is that ranking of taxa is arbitrary. This is, apparently, not obvious. Phenetics claims to be "objective" or "non-arbitrary" by measuring similarities and ranking clusters on some unweighted mathematical basis (Sneath and Sokal 1973). However, what "similarity" is, other than a more or less intuitive judgement, has never been explained (see Hull 1970). Further, the choice of the mathematical technique must, ultimately, be as arbitrary as any judgement by a conventional taxonomist. Ghiselin (1969, p. 21) points out that "mathematics can reasonably be treated as a branch of logic, and to view any form of logic as something more mysterious or valid than what is called common sense is without foundation and smacks of the superstition of numerology. Scientific inferences should be accepted because the premises are true and because the conclusions follow logically. The truth does not derive from the jargon in which it is expressed." It is evident that the philosophical and theoretical bases of computer taxonomy are weak (e.g., Hull 1970); therefore one is not to accept their assertions merely because mathematics is used.

Cladists have attempted to rank taxa on the basis of times of splitting. This might, in theory, be nonarbitrary, but for the vast majority of organisms the fossil record is so poor as to provide few clues as to times of origin. It is true that similarities between taxa can be used to infer times of splitting, but without confirmation from fossils and stratigraphy such inferences must be weak. Selection alone directs evolution and rates of change are irregular and difficult of estimation. It is surprising that cladists tend to work with organisms lacking an adequate fossil record (Brundin 1966 [insects],

Hennig 1966 [insects], Nelson 1969, 1970 [fishes])). Certain theorists have recognized this contradiction (Nelson 1970, 1973) and attempted to negate the use of fossils and stratigraphy in the reconstruction of phylogeny. Although such concepts follow necessarily from strict adherence to cladistics, they can originate only from lack of appreciation of the scientific method, of the fossil record, and of the work of paleontologists.

In order to rank taxa "objectively" on times of splitting, cladists are forced to (arbitrarily) reject the patristic component of evolution. To incorporate real ancestors and patristic features into a general purpose classification, a flexible system of ranking is needed. Raup and Gould (1974) have demonstrated that random selection and splitting can produce an ordered, seemingly hierarchical system. Brundin (1972a, p. 72) speaks of nature producing "a system of its own that is in principle hierarchic." However, this appearance is owing to our interpretation of phylogeny from the present perspective. Nature is a complex system resulting from speciation and divergence, not an ordered hierarchy. We must, therefore, attempt to produce a labelling system for this complexity — based on scientific theory and inquiry and, ultimately, a little bit of art (Simpson 1971). Ranking must be to a greater or lesser degree arbitrary and it should cause little concern that a family of insects is not equivalent to a family of salamanders. Each has been following its own evolutionary pathway for millions of years as a different kind of animal. Evolution has not made them equivalent, why should we wish to do so artificially?

"It is preferable to consider evolutionary classification not as expressing phylogeny, not even as based on it (although in a sufficiently broad sense that is true), but as *consistent* with it. *A consistent evolutionary classification is one whose implications, drawn according to stated criteria of such classifications, do not contradict the classifier's views as to the phylogeny of the group*" (Simpson 1961, p. 113, italics original). An evolutionary classification is consistent with phylogeny (both of its aspects) and therefore a reflection of evolutionary theory. It is also a stable, flexible cataloguing system, well suited to everyday use by all biologists. In these things it remains the optimal system, preferable to both cladistic and phenetic taxonomy, but capable of using the methods of both. It would seem that if Simpson (1945, 1961) were read and, more importantly, understood, fewer controversies would result. For evolutionary biologists, the logical theory of systematics must be evolutionary. Cladistic and phenetic analysis of phylogeny can be powerful tools (depending on the circumstances), but let us not confuse tools with theory or phylogenetic research with classification.

C. History of Classification of the Caudata

In order to better understand present methods and principles of classification, it is helpful to know the systems used in the past. Knowledge of the historical development of the classification of the Caudata may help reduce biases and prevent repetition of past errors. During the earlier stages of work on a higher taxon, the choice of "significant" or "meaningful" taxonomic characters is empirical and,

at least in retrospect, subjective. As the group becomes better known, the classification changes and the subjective component perhaps decreases, but can never be totally absent.

The class Amphibia of Linnaeus (1758) united amphibians and reptiles, as well as lampreys, sharks and rays, and the sturgeon. These organisms were divided into Reptiles (including salamanders and lizards in the single genus *Lacerta*, all anurans in the genus *Rana*, turtles, and crocodiles), Serpentes (all snake-like tetrapods), and Nantes (the various included fishes). Somewhat later, Laurentius (1768) used three orders in a class Reptilia: Salientia (frogs and toads), Gradientia (salamanders [in two genera, *Triton* and *Salamandra*], lizards, and crocodiles), and Serpentina (snakes, apodans, and amphisbaenians).

Other classifications for the amphibians and reptiles were proposed during the late 1700's (see Kuhn 1967), but Oppel (1811) was apparently the first to place all amphibians in a single unit. This order, however, was still classified in the class Reptilia as follows:

Class Reptilia

Order Testudinata (turtles and tortoises)

Order Squamata

Section Saurii (crocodiles and lizards)

Section Ophidii (snakes and amphisbaenians)

Order Nuda

Family Apoda

Family Ecaudata (anurans)

Family Caudata.

In modern terms the Order Nuda (= Amphibia) is natural at the higher levels: the relationship of the three included families to each other

and their distinction from reptiles is clearly shown. Subsequent workers generally agreed that amphibians and reptiles were different, although both were united in a single class.

Gray (1825, p. 194) noted that the Amphibia and Reptilia "are allowed to be perfectly distinct by all modern naturalists," and divided the Amphibia as follows:

Class Amphibia

Mutabilia (undergoing metamorphosis)

Order Anoura

Family Ranidae (all frogs and toads)

Order Urodela

Family Salamandridae (all known metamorphosing salamanders in the genera *Triton* and *Salamandra*)

Amphineusta (lacking metamorphosis)

Order Sirenes

Family Sirenidae (*Siren*, *Pseudobranchius*, *Proteus*, *Necturus*)

Family Amphiumidae (*Amphiuma*, *Cryptobranchus*)

Order Apoda

Family Caeciliadae.

In this classification, the presence or absence of transformation was used to divide the salamanders: one group being placed with the frogs and toads, the second comprising the fully aquatic (paedogenic) species and the caecilians. Although perhaps bizarre by present standards, given the state of the art, there was no reason to reject such a division. The theory of evolution was not available to provide an acceptable definition for a natural system of classification. Gray's classification is "good" in that it is based on observable features and in serving to distinguish subgroups of Amphibians.

Gray (1825, p. 216) placed *Amphiuma* and *Cryptobranchus* in a single family, which was defined as follows: "Branchia none, skull formed of

solid bony substance; gill flaps open during life; body subcylindrical; tail compressed; legs four." Although different from present classifications, which are based on additional data and differing interpretations, Gray's Amphiumidae was based on characters that are factually correct. Only in light of our different theories and weighting of characters does the scheme become wrong.

Tschudi's (1838) *Classification der Batrachier* greatly influenced subsequent workers. He divided the Amphibia into four orders: Batrachia (frogs and toads), Cacaelia, Salamandrinae, and Proteideae. The Salamandrinae included four-footed, tailed animals, lacking external gills in the adult. The Proteideae were salamanders with elongate heads, large upper lips, external gills present or absent in the adult, and a laterally compressed tail. These two orders were subdivided as follows (modern generic and specific names substituted as necessary);

Class Amphibia

Order Salamandrinae

Family Salamandreae (tail round or roundish)

Content: *Hynobius naevius*, *Onychodactylus*, *Ambystoma maculatum*, *Plethodon*, *Eurycea*, supergenus *Bolitoglossa*, *Salamandra*, *Salamandrina*.

Family Tritones (tail laterally compressed, often high)

Content: *Hynobius nebulosus*, *Ambystoma jeffersonianum*, *Hydromantes*, *Hemidactylium*, *Pseudotriton*, *Cynops*, *Triturus*, and their allies.

Family Tritonides (head flat and robust; eyes small; tail laterally compressed)

Content: *Cryptobranchus*.

Order Proteideae

Content: *Ambystoma mexicanum*, *Amphiuma*, *Necturus*, *Proteus*, *Siren*, *Pseudobranchus*.

Although there is inconsistency in the separation of the Salamandreae from the Tritones, the classification is "good" in terms of providing taxa that are otherwise well differentiated.

Fitzinger (1843) placed amphibians in one of five Series within the class Reptilia. Following Gray (1825), he united caecilians and some of the salamanders in a single order. Although Fitzinger did not diagnose the amphibian taxa, the names of the subsections provide clues to the reasoning used: His classification is as follows:

Class Reptilia

Series Dipnoa (= Amphibia)

Order Batrachia (frogs and toads)

Order Hemibatrachia (transforming salamanders)

Section Phaeneropleurae

Family Pleurodelae

Content: *Pleurodeles*.

Section Cryptopleurae

Family Salamandrinae

Content: *Salamandrina*, *Cynops*, *Euproctus*.

Section Geophili

Family Salamandreae

Content: some hynobiids, some *Ambystoma*, most of the then known plethodontids, *Salamandra*.

Section Hydrophili

Family Tritones

Content: some *Hynobius*, *Ambystoma jeffersonianum*, *Pseudotriton*, *Triturus*.

Order Ichthyodea

Section Hemisalamandreae

Family Megalobatrachi

Content: *Cryptobranchus scheuchzeri*, *C. japonicus*.

Section Derotremata

Family Salamandropes

Content: *Cryptobranchus alleganiensis*.

Family Muraenopses

Content: *Amphiuma*.

Section Anura (caecilians)

Section Branchiata

Family Necturi

Content: *Ambystoma mexicanum*, *Necturus*.

Family Sirenes

Content: *Siren*, *Pseudobranchius*, *Proteus*.

Hallowell (1856) classified the caducibranchiate salamanders (those losing the gills at metamorphosis) in nine families, based largely on the structure of the tongue. This arrangement was as follows (Hallowell 1856, pp. 10-11, modern generic and specific names substituted when necessary);

Group A, having longitudinal teeth on the palate:

Family Salamandridae ("Tongue rather large, attached in front and posteriorly, free at the sides; toes 4-5.")

Content: *Salamandra*.

Family Seiranotidae ("Tongue well developed, oblong, rounded in front and almost truncate posteriorly, *free in its posterior half*, less so laterally, attached in front, toes 4-4.")

Content: *Salamandrina*.

Family Pleurodelidae ("Tongue small, subcircular, *free posteriorly*, and at sides, attached in front; toes 4-5.")

Content: not given.

Family Tritonidae ("Tongue fleshy, papillose, well developed, *attached in front and behind*, free at the lateral edges; toes 4-5.")

Content: *Triturus*, *Euproctus*, *Notophthalmus*, *Taricha*, the Asian newts exclusive of *Tylototriton*.

Family Ellipsoglossidae ("Tongue oblong oval, *free at the sides only*; toes 4-5.")

Content: *Hynobius*.

Group B, having transverse and longitudinal teeth on palate:

Family Plethodontidae ("Tongue broad oval, well developed, free at its lateral edges and posteriorly, attached in front; toes 4-5.")

Content: *Plethodon*, *Aneides*, *Desmognathus*.

Family Bolitoglossidae ("Tongue of moderate size, mushroom-shaped, supported by a central pedicel; toes 4-5 and 4-4.")

Content: *Batrachoseps*, *Pseudotriton*, *Hydromantes*, "*Spelerpes*" (remainder of the free-tongued plethodontids).

Family Hemidactylidae ("Tongue oval, attached in front and along the middle, more free posteriorly; toes 4-4.")

Content: *Hemidactylium*.

Group C, only transverse teeth on the palate:

Family Ambystomidae ("Tongue ovate, moderately free at its edges, slightly so in front, attached posteriorly; toes 4-5.")

Content: *Onychodactylus*, *Ambystoma*, *Dicamptodon*.

Hallowell classified the families on the basis of the disposition of the teeth on the palate. The Hynobiidae, some species of which have transverse rows and others longitudinal rows of teeth, were not recognized. Except for this, and the splitting of the presently recognized Salamandridae into four and the Plethodontidae into two families, Hallowell classified the Caudata in groups considered natural today.

In a second classification, Gray (1858) noted the variability of external features in salamanders and used cranial structure as the major diagnostic character complex. This, by implication, indicates recognition of the necessity for weighting characters. Gray considered the frontosquamosal arch of major importance for a natural classification of the Caudata. He divided the Salamandridae of present usage into

three families, erected the Molgidae for *Hynobius naevius*, and placed ambystomatids, plethodontids, and the majority of hynobiids in the family Plethodontidae.

In the following year, Cope (1859) published a classification of the caducibranchiate salamanders as follows:

Order Caducibranchiata (gills lost at metamorphosis)

Suborder Urodela

Family Protonopsidae ("Branchial apertures persistent.")

Content: not given.

Family Salamandridae ("Branchial apertures none.")

Subfamily Ambystominae (lacking "parasphenoid" teeth,
palatine teeth in a transverse series on
elevated parts of the vomer)

Content: *Onychodactylus*, *Cryptobranchus japonicus*,
Ambystoma.

Subfamily Spelerpinae (numerous parasphenoid teeth, plus a
short transverse series of vomerine teeth)

1. Plethodontae (tongue attached)

Content: *Plethodon*, *Aneides*, *Desmognathus*.

2. Spelerpeae (tongue free)

Content: free-tongued plethodontids.

Subfamily Hynobiinae (vomerine teeth said to be lacking,
"parasphenoid" teeth in two anteriorly diverging
rows)

Content: *Hynobius*.

Subfamily Salamandrinae (vomerine teeth on inner surfaces of
vomeres, which are elongate and posteriorly
divergent)

1. Salamandrae (vomerine teeth "cuneiform," ribs claimed
lacking)

Content: *Salamandra*.

2. Pleurodelae (vomerine teeth "cuneiform," ribs large)

Content: *Salamandrina*, *Pleurodeles*.

3. Tritones (vomarine teeth "cuneiform," ribs claimed lacking)

Content: remainder of the newts then recognized.

Cope wrote (1859, p. 122) that: "The characters of the . . . subfamilies are taken from the position, etc., of the palatine and sphenoidal teeth, and we are of the opinion that the groups thus formed will be found to be more natural than those established exclusively upon the form of the tongue." These characters did serve to separate the metamorphosing salamanders into more or less their presently accepted families (called subfamilies by Cope). While arguing that his classification was more "natural" than those based only on the "form of the tongue" (probably a reference to Hallowell 1856), Cope was not explicit as to what "natural" might mean.

Having chosen the presence or absence of gill slits in the adult as the character used to separate the Urodela into two families, Cope (1859, p. 122) was forced to place the cryptobranchid species into two different families, stating that "the great aquatic salamander of Japan is closely allied to our *Protonopsis* [= *Cryptobranchus alleganiensis*] . . . but the absence of branchial slits places it among the true Salamanders." This is, at least, consistent and selection of characters is difficult in the absence of evolutionary theory.

Cope (1867) published a more detailed and rigorous classification, which was based on a series of primarily osteological characters. Cope criticized the use of Perennibranchiata (gilled adults) and Caducibranchiata (gills lost at metamorphosis), noting *Siredon* (= *A. mexicanum*) was known to metamorphose into *Ambystoma*, the resemblance of *Necturus* to larval plethodontids, and the variable development of gills

in *Siren*. He recognized that separation of the caducibranchiates into those with and without gill slits (as he had done previously [Cope 1859]) was not justified, stating that "this feature is of no greater value than any other, as the very closely allied genera *Protonopsis* [= *C. alleganiensis*] and *Megalogatrachus* [= *C. japonicus*] differ in this respect" (Cope 1867, p. 104). Cope's order Urodela included three suborders: the Trachystomata (for the Sirenidae), Proteida (Proteidae), and Caducibranchiata (the remaining families). Of the Caducibranchiata, Cope (1867, p. 102) stated: "This name, although not strictly applicable to Siredons included in the suborder may be retained." Caducibranchiate salamanders were divided into eight families as follows:

- A. Family Amphiumidae (as presently recognized)
- B. Family Protonopsidae (= Cryptobranchidae)
- C. Family Amblystomidae (= Ambystomatidae plus *Onychodactylus*)
- D. Family Plethodontidae (as presently recognized, exclusive of the Desmognathini)

Family Desmognathidae (= Desmognathini)

- E. Family Hynobiidae (as presently recognized, minus *Onychodactylus*)
- F. Family Salamandridae (*Salamandra*, *Triturus cristatus*)
- Family Pleurodelidae (= Pleurodelinae, minus *T. cristatus*).

In comparison to this classification, that of Boulenger (1882) represents in retrospect a major regression. Boulenger separated the order Caudata into four families: the Proteidae and Sirenidae were as presently recognized; the Amphiumidae included *Amphiuma* and *Cryptobranchus*; and the Salamandridae was divided into four subfamilies. The Amphiumidae were distinguished on the absence of external gills and eyelids in the adult, the presence of maxillae, and the possession of amphicoelous vertebrae. The Salamandridae were divided as follows:

1. Salamandrinae (= Salamandridae as presently recognized)
2. Amblystomatinae (Hynobiidae and Ambystomatidae)
3. Plethodontinae (Plethodontinae of Wake 1966)
4. Desmognathinae (Desmognathinae of Wake 1966).

Although different from those of today, these older classifications are constructed in a similar manner. Characters that are distinctive and allow for the separation of species into more or less well-defined groups continue to be used in classification. Although we have the theory of evolution as a unifying principle, many taxonomic characters are still chosen on an empirical basis (see Darwin 1859). The old classifications should not be viewed in the context of our present, "correct" systems as naive attempts to order salamanders. They must be judged on their own merits as to whether they are internally consistent and follow from data then available. On this basis, many of the older schemes are admirable. After Boulenger (1882), who can be taken as the last of the old taxonomic school, the classifications become more recognizable.

Cope (1889) proposed a modified classification in his report on *The Batrachia of North America*. Three orders were used to hold the subordinate taxa, whereas one had been sufficient previously (Cope 1867). This classification is as follows:

1. Order Urodela
 - Suborder Apoda
 - Suborder Trematodera
 - Family Cryptobranchidae
 - Suborder Amphiumoidea
 - Family Amphiumidae

Suborder Pseudosauria

Family Amblystomidae

Family Hynobiidae

Family Plethodontidae

Family Desmognathidae

Family Thoriidae

Family Pleurodelidae

2. Order Proteida

Family Proteidae

3. Order Trachystomata

Family Sirenidae.

This classification does not differ profoundly from those presently in use. Cope (1889) split the Plethodontidae into three families and the Salamandridae into two. The Proteida were separated from the Urodela on the basis of the unique presence of the large opisthotic (Cope's *os intercalare*). Cope believed this indicated that proteids were intermediate between the stegocephalians and other salamanders. Sirenids were placed in a distinct order Trachystomata, which was suggested to be derived from the Urodela.

The next major contribution was proposed by Dunn (1922), in which the families are those still recognized and arrangements of the taxa are similar to those of today. The classification was based on several characters and is as follows:

Order Caudata

Suborder Mutabilia

Superfamily Salamandroidea

Family Ambystomidae

Family Salamandridae

Family Plethodontidae

Superfamily Amphiumoidea

Family Amphiumidae

Superfamily Cryptobranchoidea

Family Hynobiidae

Family Cryptobranchidae

Suborder Proteida

Family Proteidae

Suborder Meantes

Family Sirenidae.

Cope's (1889) continuing influence is seen in the three-way division of the Caudata into the Mutabilia (Cope's Urodela), Meantes (Cope's Trachystomata), and Proteida. Hynobiids and cryptobranchids are still placed in the Cryptobranchoidea, even though this grouping is based on primitive features. Sirenids and proteids were separated into their own suborders owing to uncertainty as to their true relationships.

Dunn (1922, p. 421) explicitly stated that "classification should be based upon all available characters, so that possible parallelisms will not lead to wrong conclusions." He (1926) subsequently modified this classification, splitting the Caudata into three suborders: the Meantes and Cryptobranchoidea, which contained the same families as before, and the Salamandroidea, into which all other families were placed.

In the *Biology of the Amphibia*, Noble (1931) provided the classification that was to stand basically unaltered until the late 1960's. He included detailed diagnoses of the suborders and families, as well as a phylogenetic reconstruction for the order (Noble 1931, fig. 145). The classification is as follows:

Order Caudata

Suborder Cryptobranchoidea

Family Hynobiidae

Family Cryptobranchidae

Suborder Ambystomoidea

Family Ambystomidae

Suborder Salamandroidea

Family Salamandridae

Family Plethodontidae

Family Amphiumidae

Suborder Proteida

Family Proteidae

Suborder Meantes

Family Sirenidae.

Although Noble's ideas of the Salamandroidea are not accepted by present workers (e.g., Regal 1966, Wake 1966), the character used to unite them is real and readily observable. Noble (1931, p. 473) defined salamandroids as comprised of "metamorphosing urodele[s] having teeth on the roof of the palate well behind the internal nares." This is now interpreted as owing to convergence in all three families.

Laurent (1947) pointed out the fundamental difference in the situation of the vomerine teeth between salamandrids and plethodontids. Whereas salamandrids have longitudinal palatal teeth formed of posterolateral extensions of the tooth-bearing parts of the vomers, plethodontids have parasphenoid tooth patches produced by posterior migration of teeth from the medial portion of the vomer (see Regal 1966). Laurent (1947) also noted that plethodontids usually retain a septomaxillary, have well-developed costal grooves, lack a fronto-squamosal arch, and usually have amphicoelous centra; characters which differ from those of the majority of salamandrids.

In a detailed study, which has unfortunately not been published, Larsen (1963) proposed a new system of relationships for the Caudata. Following Laurent (1947), he considered plethodontids to be best referred to a separate suborder, the Plethodontoidea, derived independently from hynobiid ancestry and not closely related to salamandrids. Larsen suggested that amphiumids were derived from salamandrids, sirenids from plethodontids, and that proteids evolved from "prohynobiid" ancestry prior to the origins of the other families. The data for these conclusions primarily came from cranial osteology, although other evidence was also considered.

Monath (1965) suggested further revisions, and Regal (1966) proposed a new classification, as follows:

Order Caudata

Suborder Cryptobranchoidea

Family Cryptobranchidae (hynobiids and cryptobranchids)

Family Ambystomatidae

Family Plethodontidae

Suborder Amphiumoidea

Family Amphiumidae

Suborder Proteida

Family Proteidae

Suborder Meantes

Family Sirenidae.

This classification is based primarily on the dispositions of the vomerine teeth, although Monath's (1965) work on the auditory apparatus supported unification of plethodontids and ambystomatids in a common suborder. Regal (1966) suggested that the Amphiumidae were probably closest to ambystomatids and plethodontids, without noting that his primary character (the vomerine teeth) would controvert such a

relationship. Of note in this classification is the rejection both of breeding behavior and primitive cranial features as a basis for separation of hynobiids and cryptobranchids into a distinct suborder. Except for the relationship between ambystomatids and plethodontids, Regal's arrangement has not been accepted, undoubtedly in large part because it ignores the primary dichotomy between cryptobranchoids and the remainder of the Caudata.

Wake (1966) included a classification of the families of salamander in his study of the Plethodontidae. This differed from that of Regal in recognizing the Cryptobranchioidea in the sense of Noble (1931), including plethodontids and ambystomatids in the Ambystomatoidea, classifying *Necturus* and *Proteus* in separate families with salamandrids and (questionably) amphiumids in the Salamandroidea, and changing the name Meantes to Sirenoidea. Justification for the arrangement of the families was not provided.

Wake (1966, p. 74) suggested that the "suborders Ambystomatoidea and Salamandroidea represent separate evolutionary lines that have diverged independently from an ancestral stock similar to modern hynobiids." This statement is controverted by evidence from the vertebral column and trunk musculature (see above), and it also ignored several important shared-derived characters known at the time. Nevertheless, this classification seemed to reflect knowledge of the interfamilial relationships of the Caudata and has been the one most utilized since.

A recent reorganization of the salamanders was proposed by Edwards (1976):

Order Caudata

Suborder Cryptobranchoidea

Family Cryptobranchidae

Family Hynobiidae

Suborder Sirenoidea

Family Sirenidae

Suborder Proteoidea

Family Proteidae

Suborder Batrachosauroidoidea

Family Batrachosauroididae

Family Prosirenidae

Suborder Amphiumoidea

Family Amphiumidae

Suborder Ambystomatoidea

Family Dicamptodontidae

Content: *Dicamptodon*, *Rhyacotriton*, scapherpentontids.

Family Ambystomatidae

Content: *Ambystoma*, *Rhyacosiredon*.

Family Plethodontidae

Suborder Salamandroidea

Family Salamandridae.

The major distinctions of this classification are the new family Dicamptodontidae and the unification of batrachosauroidids and prosirenids in a single suborder. I disagree with the changes proposed by Edwards and a discussion is found below (see Conclusions).

Consideration of the historical development of the classification of the Caudata is instructive. The earlier attempts to attain "natural" classifications were necessarily based on differing philosophical standards (pre- and post-Darwinian). Multicharacter classifications based on reasoned arguments as to the relative importance of the various characters gradually developed. Early workers

attempted to set up schemes based on single distinguishing characters (e.g., Gray 1825), whereas the later ones (e.g., Cope 1867, 1889) utilized suites of traits in classifying. The change was probably aided by the impact of evolutionary theory and Darwin's detailed consideration of taxonomic problems.

Darwin (1859, p. 417) wrote that "it has been found, that a classification founded on any single character, however important that may be, has always failed." He noted (p. 415) that "almost all naturalists lay the greatest stress on resemblances in organs of high vital or physiological [i.e. functional] importance. [But] . . . the mere physiological importance of an organ does not necessarily determine its classificatory value . . . [as] in allied groups, in which the same organ . . . has nearly the same physiological value, its classificatory value is widely different." The important point is constancy of development, with "a character nearly uniform, and common to a great number of forms, and not common to others, . . . [being used] as one of high value" (Darwin 1859, p. 418).

Chapter IV

CONCLUSIONS

A. Functional Morphology

i) Introduction

In this section data gained during this study are used to make suggestions as to the functional reasons for certain structures. As these hypotheses are derived almost solely from dissection of preserved material, they are tentative. Comparative anatomy as a sole or major tool in the study of function has been criticized, but I believe it to be a valuable aid.

Gans (1966, p. 46) argues that, in general, function cannot be derived from the study of structure and that: "Functional morphology on the basis of deduction from structure should then be restricted to rare animals or fossils, on the assumption that it may be possible to derive some information from "similar" forms." This is basically correct, but in practice comparative anatomy would seem to necessarily come before functional morphology. That is, the first step in functional morphology is the formulation of hypotheses from information based on the study of structure (see Regal and Gans 1976, Lombard and Wake 1976, for such preliminary steps).

Gans (1966, p. 45) states that there are three assumptions to be accepted in order to allow (in theory) elucidation of function from structure. These are as follows:

"(1) that the architecture of an element is molded primarily by present function,

(2) that a given structure is in the grip of a single over-riding function, and

(3) that a structure will incorporate an equal factor of safety (or no factor of safety) in all directions and versus all kinds of adaptation induced stresses."

Gans then argues that each of these assumptions is invalid, which is partially correct. I would also agree that definitive functional morphology is not possible based only on comparative anatomy of preserved material. However, comparative anatomy must come prior to studies of living animals, so as to elucidate potential functional relationships, which can then be tested.

Whereas it cannot be argued that detailed functional interpretations can be based solely on structure, it is possible to arrive at relatively detailed hypotheses from strictly structural studies. It is reasonable, I suggest, to assume "that the architecture of an element is molded primarily by present function" (Gans 1966, p. 45), so long as the statement is qualified. Dichotomy of structures into those owing to immediate adaptation and those owing to descent is all but completely artificial, as shown by Cain (1964). All existing structures are, to a greater or lesser extent, owing to descent, but also, almost invariably, to immediate functional requirements. Retention of a structure derived from some ancestor is based on continuing selection, loss of function leading to loss of the structure. Historical factors are extremely important, but not because they force a lineage into inadapative or suboptimal states. Structures and functions already present necessarily influence and canalize future

change by their interactions with natural selection, but the first assumption of Gans is still very reasonable.

The validity of the other assumptions depends on the role that is assigned to the elucidation of function from structure. Gross errors are possible, and small errors inevitable, if it is attempted to deduce all possible functions from the structure of a system. However, there is surely no need to assume (operationally or theoretically) a one structure-one function relationship. If it is recognized that structures often have multiple functions, comparative anatomy remains a powerful (and indispensable) tool in the study of function.

Comparative anatomy allows one to understand what structures are present and to formulate generalizations and hypotheses of probable actions and functions. "Partitioning the several kinds of similarities [homology, analogy, and homoplasy] is likely to be most successful when one is simultaneously comparing as many members as possible from what appears to be a single adaptive radiation" (Gans 1974, p. 18). On this basis, the sort of functional morphology advocated by Gans (1966, 1974) may then be carried out.

Gans' (1974) *Biomechanics* exhibits this approach very well, perhaps in contrast to his more theoretical treatment published earlier (Gans 1966). It incorporates functional studies on "intact" animals as well as detailed considerations of structure. Regal and Gans (1976) provided comparative anatomical descriptions of frog tongues. Such a study and its functional speculations then serve as the first step prior to more detailed functional studies (see also Lombard and Wake 1976).

Studies such as mine on the trunk musculature and vertebral column of salamanders potentially open further possibilities for functional morphology. Elucidation of how species of different genera and families differ structurally allows comparison of their natural histories and inferences of possible explanations and correlations. These can then be tested and expanded by studies of living animals, as urged by Gans (1966, 1974). Unless one knows precisely what structures are present and their intra- and interspecific variations, experimental functional morphology, even if possible, is sterile.

ii) Interpretations

Transverse processes and ribs.— Noble (1931) proposed that bicipital ribs in salamanders function to resist the downward pull of gravity on the viscera in terrestrial situations. Certain facts seem to support this suggestion: for example, aquatic salamanders tend, on average, to have closely appressed rib-bearers (e.g., *Cryptobranchus*). However, other facts stand in contradiction. Frogs lack bicipital ribs and rib-bearers, usually retaining only somewhat elongated transverse processes. In these animals the belly hangs down as a large bag, supported by only a small amount of lateral and ventral abdominal musculature. Also, rather than being oriented vertically, as in salamanders, these transverse processes are more or less horizontal and dorsoventrally flattened. In salamanders the ribs and rib-bearers are almost invariably most bicipital anteriorly, in the region of the pectoral girdle. In the posterior region of the trunk, where the viscera are concentrated, they are generally less strongly bicipital.

Musculature would seem sufficient to hold in the contents of the abdominal cavity. Finally, it is to be noted that the ribs are usually completely enclosed within the *dorsalis trunci* and *subvertebralis*, which indicates that ribs do not function directly in support of the viscera. Lizards, which are more fully terrestrial and often much larger than salamanders, do not show the bicipital ribs and transverse processes seen in urodeles.

I suggest a different explanation for the presence of long rib-bearers and bicipital ribs: in salamanders the transverse processes and ribs are functioning as integral parts of the myosepta separating the myomeres. The transverse processes and proximal heads of the ribs are oriented in conformity with the slope of the myomeres, serving as rigid (in the case of the transverse processes) or semi-rigid (in the case of the ribs) sites of attachment for muscle fibers.

Owing to the mechanism of the buccal pump in lung ventilation (Gans 1974), elongate transverse processes in salamanders are possible. This contrasts with lizards, mammals, and labyrinthodonts in which the ribs are mobile directly on the centrum without an intervening transverse process (see Romer 1966). In these sorts of animals the ribs function for costal pump ventilation as well as in locomotion. However, in salamanders the transverse processes and ribs function only in locomotion. The transverse processes align with the myosepta and the ribs form movable lateral extensions from them. Such transverse processes serve as solid sites of attachment for muscle fibers so as to allow for short bursts of rapid movement. Urodeles spend much time at rest, moving quickly and suddenly only to capture prey (when in the

water) or to escape predation. Movement is often rapidly initiated and quickly terminated. Similar habits are also exhibited by the fish *Amia* and *Lepisosteus*, both of which also have transverse processes.

This model should have significance for inferences about Paleozoic amphibians. The sort of rib articulation should indicate whether a buccal or costal pump was being utilized, and allows inferences as to how the organisms were living. Unfortunately, such suggestions are often made on the basis of little, or incorrect, evidence from living organisms.

Opisthocoely. (see Figs. 93-97).- There has been no satisfactory hypothesis proposed to account for the presence of amphicoely and opisthocoely in the different families of salamanders. The problem may be considered in two parts:

1. Why are some salamanders amphicoelous and some provided with a ball-and-socket intercentral joint?
2. Why are all salamanders provided with a ball-and-socket joint opisthocoelous and none procoelous?

Information from the study of the trunk musculature of representatives from all of the living families of salamanders, and of dissections of certain lizards, can be used to help answer these questions.

Wake (1966, p. 57) concluded that the "development of opisthocoely facilitates increased intervertebral movement, the result of increased trunk and tail flexures." The first part of this suggestion is partially true, the second part is controverted by various facts and overlooks certain correlations. If true, Wake's suggestion would seem to indicate that the more flexible salamanders should be opisthocoelous.

Cryptobranchids, amphiumids, sirenids, and proteids are, however, fully amphicoelous. Further, it is likely that the latter two families are derived from opisthocoelous ancestors (see below), being secondarily amphicoelous.

Snakes might superficially seem to provide support for Wake's theory. However, these reptiles require a column that is both flexible and strong, therefore requiring smooth ball-and-socket joints. An amphicoelous snake, although highly flexible, would lack the strength necessary for such a relatively large, active, terrestrial vertebrate. Snakes also have numerous, rather short vertebrae to increase flexibility. Among fish, only the relatively rigid gar-pike (*Lepisosteus*) has non-notochordal vertebrae (which are opisthocoelous).

Data from anurans also controvert the suggestion that the ball-and-socket joint in amphibians is to increase flexibility. These amphibians have developed a rigid column owing to the pressures imposed by saltatory locomotion. During the jump the column must be held stiff, allowing force to be concentrated in one direction (i.e., a flexible arrow is nonfunctional). Therefore, the column is strengthened by ball-and-socket joints and long transverse processes. Although the ascaphids have amphicoelous vertebrae, this exception further strengthens the argument. *Ascaphus* and *Liopelma* frequent streams, being highly aquatic and indifferent jumpers. *Ascaphus* is "sluggish," a poor jumper, and swims "rather slowly, frequently using . . . [the] hind legs alternately" (Stebbins 1962, p. 90).

I suggest that the primary factor causing selection for a ball-and-socket joint has been (and is) the need for strength, not

flexibility. The system can certainly maintain flexibility, but this is not the reason for its initial development. This contention is supported by several lines of evidence from the Caudata.

The highly flexible, aquatic salamanders are invariably amphicoelous, with relatively large amounts of trunk musculature. The trunk musculature of amphicoelous species is generally also constructed so as to displace the area of contraction laterally, away from the column. This is part of the function of the marked folding of the septa of the *subvertebralis* and *dorsalis trunci* in most amphicoelous species, which is carried to an extreme in the anguilliform *Amphiuma* (see Figs. 28, 29, and 30). In this manner the force of contraction is displaced so as to decrease the direct pull on the vertebral column and thus reduce the strain on each intercentral joint.

By contrast, those urodeles that develop opisthocoely have a more direct association of musculature to individual vertebrae and a marked decrease in the amount of septal folding. Structural mechanisms to decrease strain on the intercentral joints are reduced or lacking. Individual muscle sections tend to insert discretely on the vertebrae, at which points accessory projections for origins and insertions are often developed. For example, *Desmognathus* has well-developed posterior basapophyseal muscles, pterygapophyseal muscles, and hyperapophyseal muscles (see Fig. 67), as well as the associated structures on the vertebrae (see Figs. 1 and 16). This genus also has an anterior hyperapophyseal projection situated between the posterior basapophyses of the next anterior vertebra, seemingly to augment the condyle in preventing intercentral dislocation. The salamandrid newts exhibit

marked reduction in the complexity of the *subvertebralis*, the fibers being strictly intervertebral with no overlap, and the *transversus* inserting medially on the centra. Newts reduce the complexity of the *dorsalis trunci* (compare *Taricha* and *Ambystoma*), concentrating stress more directly on the column. This concentration is also evidenced by the high neural crests, aliform processes, and associated musculature. Although *Siren* is very similar in these features to the newts, it differs in the larger mass of axial musculature burying the column and, presumably, cushioning the joints. Newts show remarkable convergence in the structure of the *transversus* and *subvertebralis* with the procoelous lizards (see Fig. 97).

In amphicoelous species having anterior basapophyseal musculature, the anterior basapophyseal muscles are generally not intimately attached to the anterior basapophyses. These muscles are loosely connected to the centrum medially and are probably more properly part of the posterior (transverse process) flexures in a functional sense. By contrast, urodeles with posterior basapophyseal muscles (derived from the posterior flexures) tend to have well-developed, sometimes greatly enlarged, posterior basapophyses. The muscles associated with these projections are more differentiated in the sense of being separated from the more lateral parts of the *subvertebralis*, placing more direct pull on the vertebrae and intercentral joints than is the case in salamanders with anterior basapophyseal musculature.

Amphicoelous salamanders are generally highly aquatic, short-bodied, provided with relatively bulky trunk musculature, and/or relatively small. These factors indicate a lessened strain on the intercentral

joints. Certain plethodontids show development of a so-called "functional" opisthocoely in larger, older individuals (see Moore 1900). In such cases the anterior cotyles extend partially into the posterior cotyles of the associated vertebrae. This suggests that the change in vertebral articulation ontogenetically occurs owing to the necessity for strengthening the joints against disarticulation. Certainly there can be no increased demand for flexibility as the animal gets larger, nor could the kind of joint produced provide for increased flexibility.

By contrast, desmognathines have a fully developed, true opisthocoely (Moore 1900). This condition in relatively small-limbed, elongate animals might seem to run counter to the argument being developed. However, the habits, cranial osteology, and musculature of these salamanders show adaptation to burrowing (see Hinderstein 1971, Wake 1977). I have observed adult *Desmognathus fuscus* displace relatively large rocks as they move under them. It would seem reasonable that the vertebral column and its associated musculature are co-adapted with the skull and correlate with these habits. Although the column is certainly flexible, there has also been selection for its strengthening, as shown by the accessory processes on the vertebrae. In this case, in order to maintain flexibility and to strengthen the column, opisthocoely has developed. This is, however, not owing to need for increased flexibility.

The conditions obtained in the extinct batrachosauroidids (including *Prodesmodon*, see Naylor 1978a) might seem difficult to explain. The paedomorphic skull, elongate body (where known), and small limbs might be interpreted as more properly associated with

amphicoelous centra. However, it is probable that batrachosauroidids were burrowers. There are stalked occipital condyles on the skull (see Estes 1969a, 1975), as in *Desmognathus*, and the atlas bears resemblances to that of *Amphiuma*. This indicates well-developed cranio-mandibular musculature and powerful dorsoventral movements of the head. The elongate body and small limbs (where known) are also traits correlated with burrowing. Finally, there is a good structural cline leading through the condition of the vertebrae in *Prodesmodon* and *Opisthotriton* to that of *Palaeoproteus* and *Batrachosauroides*, documenting reduction in the relative size and strength of the opisthocoelous ball. If this can be taken to reflect an actual phylogenetic event, it could indicate evolution away from a primarily burrowing way of life towards a more strictly swimming existence and, therefore, the reduction of opisthocoely.

In hynobiids, cryptobranchids, ambystomatids, proteids, and certain plethodontids, the vertebral column functions as a sort of special "notochord." That is, there is relatively little direct pull on the vertebrae. This is indicated by the dissections described above and by the general lack of distinct accessory projections from the vertebrae. In these salamanders, the column appears to be bent in a more gentle arc during locomotion than is the case in newts, as indicated by observations on living *Taricha* and *Ambystoma* and by study of preserved specimens that have been fixed in various attitudes. In addition, the structure of the axial musculature with respect to the number of flexures and the amounts of musculature suggests adaptations to concentration of pull away from the column. In salamandrids with

greater amounts of trunk musculature and relatively more distinct flexures, the ball-and-socket joints of the centra are weakened (e.g., *Salamandra* and *Pleurodeles*).

By contrast, in *Amphiuma*, *Siren*, and most newts the column is a more integral part of the axial musculature. That is, the myomeres are modified so as to exert more direct pull on the individual vertebrae. As a result the vertebrae of these species are more complex, with large, often robust neural crests, distinct basapophyses, aliform processes, alar processes, and/or subcentral keels. *Amphiuma* and *Siren* are fully aquatic, buoyed up by water, and possess large amounts of musculature distal to the column. Further, in proportion to body length, the vertebrae are foreshortened (compare *Cryptobranchus*), allowing greater flexibility but less strain on each amphicoelous joint. The trunk musculature of *Amphiuma* is readily derivable from that of hynobiids or ambystomatids, whereas *Siren* lacks this complexity. The epaxial and hypaxial musculature of the latter is very simple in comparison to that of *Amphiuma* and derivable only from an ancestor possessed of fully developed opisthocoely (see below). It thus documents reversion to amphicoely, presumably necessitated by the assumption of aquatic life and the need for a highly flexible trunk and anguilliform locomotion.

In the salamandrid newts there has been reduction in the amount and complexity of the trunk musculature, correlated with the development of strong opisthocoely. Newts have greater pull concentrated on the individual vertebrae and consequently greater stress on the intercentral joints. This stress has been compensated for by the development

of opisthocoely. It is also of note that the condyles in newts tend to have the anterior faces flattened (thus lacking a ball-and-socket joint), which might be expected if the joint is functioning to prevent dislocation, but not if it is mainly serving to increase flexibility (see Fig. 93). It is evident from the structure of the vertebrae and associated musculature that the newt vertebral column is subject to greater intervertebral strain than is the case in amphicoelous salamanders.

Although detailed observational studies utilizing x-ray movies are needed to test aspects of this framework, several statements regarding the locomotory systems of urodeles are possible. It has been shown (Roos 1964, Edwards 1977) that a walking salamander, whether newt or otherwise, generates a standing wave. There is, however, a major distinction between the swimming of amphicoelous salamanders (e.g., *Ambystoma*) and opisthocoelous ones (e.g., *Cynops*), although *Desmognathus* is a special case, being more similar to the amphicoelous salamanders. My observations indicate that in *Ambystoma* swimming involves holding the limbs against the sides and throwing the trunk and tail into waves. Swimming is sub-anguilliform, the entire body taking part. By contrast, *Taricha* and *Cynops* keep the trunk rigid during swimming, the propulsion coming from the relatively elongate, laterally compressed tail. In water, newts (*Cynops*, *Parameisotriton*, *Taricha*, and *Notophthalmus*) move primarily by walking: the column is held stiff and the limbs are used to push gently against the substrate.

The facts presented above indicate that the ball-and-socket joint is correlated with the necessity to develop a strengthened intercentral

joint. Although it maintains and may even increase flexibility, this has not been the primary reason for its evolution.

The second question, however, remains: why are no salamanders procoelous? This problem has proven open to study by means of comparative anatomy. In discussing opisthocoely and procoely in frogs, Spinar (1972, p. 184) suggested that the deciding factor "is whether the [neural] arch of a particular species connects during ontogeny with the cranial or caudal part of the future vertebra." He also noted that Fick's (1904) rule, to the effect that "the fossa always develops on the side of the joint where the tendons of the muscles are closer to the joint, but the head on the other hand develops on that articulating element which bears the tendons more distal from the joint," could be used to help explain the development of procoely and opisthocoely. Spinar (1972, p. 183) claimed that: "As a result of different locomotory specializations, procoelous vertebrae developed mostly in the forms adapted to life on dry land but opisthocoelous ones developed in those which adapted themselves to permanent life in the water."

Positioning of the neural arch during embryological development only explains how opisthocoely and procoely develop. The "why" part of the question concerns evolutionary origins and functional reasons. There does appear to be a broad correlation of procoely and opisthocoely with terrestrial and aquatic locomotion respectively, but it is likely that this is spurious. Fick's rule, however, fits extremely well with the observations gained from dissections of salamanders (see above) and is consistent with the structure of lizards and snakes. In general,

this aspect of Spinar's (1972, fig. 80) theory of the origins of opisthocoely accurately reflects the situation in salamanders that have become opisthocoelous. Posteriorly directed pull on the edges of the posterior cotyles leads to development of opisthocoely when it is necessary to strengthen the intercentral joints. This is as should be expected, with the cap (posterior cotyle) being pulled over the ball (anterior condyle).

However, Spinar's suggested origin of the procoelous condition is less satisfactory. That is, he figures tendons extending posteriorly from the anterior cotyles. In this case there would not be the same degree of force developed (in comparison to having the "tendons" extending anteriorly, as in many salamanders and at least some snakes) about the joint, and the development of procoely from such a situation is difficult to conceive. Snakes have well-developed tendons, arranged with pinnate muscle fibers, extending anteriorly from each vertebra (personal observation), in a situation analogous to that in salamanders with anterior basapophyseal muscles. Procoely, therefore, develops when there is anteriorly directed pull on the anterior cotyles.

Ambystoma maculatum, with anterior basapophyseal musculature, has a sort of "proto-procoelous" condition. The posterior cotyles are somewhat smaller in diameter than the corresponding anterior ones in larger individuals, although the condition remains fully amphicoelous. Why have not any hynobiids or ambystomatids developed procoely? Such questions are difficult to answer, and usually all that may be said is that it was not advantageous to do so. Also, the situation in

these families is such that the amount of direct pull on the anterior edge of each centrum is reduced by the close association of the anterior basapophyseal muscles with the transverse process flexures and by the amount of axial musculature, thereby reducing the inter-central stress.

Figure 94 shows the basic septal pattern of the *subvertebralis* in several more primitive salamanders. *Ambystoma jeffersonianum* has the basic, presumably primitive, pattern, from which the *subvertebralis* of other salamanders can be derived. *Amphiuma means* represents a slight modification of this pattern, simply accentuating the development of the flexures. *Plethodon jordani* is an excellent structural intermediate between the more primitive families, and those showing propensity to development of opisthocoely. It has suppressed the internal row of muscle fibers of the anterior basapophyseal muscle, but retains the latter's septum. This septum and the posterior flexure now act on the posterior edge of the posterior cotyle, however. *P. glutinosus* simply represents a continuation of this trend, with more intimate association of the posterior flexure with the posterior basapophyseal area of the centrum.

Figure 95 shows the subvertebral patterns of the more derived plethodontids: the Euryciini, Desmognathini, and an extreme form found in some Bolitoglossini and Plethodontini. *Gyrinophilus*, *Pseudotriton*, and *Desmognathus* form a clear morphocline in terms of the structure of the *subvertebralis*, leading toward development of a distinct posterior basapophyseal muscle and correlated strong opisthocoely. *Batrachoseps attenuatus* shows complete suppression of the subvertebral flexures in

a manner convergent upon salamandrids, but without the presence of opisthocoely or the migration of the origin of the *transversus* onto the centra. Why *Batrachoseps* has not developed opisthocoely as in the newts is uncertain, but perhaps it has something to do with the small body and thin trunk.

Figure 96 shows the subvertebral systems of *Necturus* and *Salamandra*, both of which have posterior flexures. However, these are not in close association with the centrum and do not form posterior basapophyseal muscles. In *Salamandra* opisthocoely is retained, whereas *Necturus* is amphicoelous, probably owing to reversion. Figure 97 diagrams the pattern seen in salamandrid newts as represented by *Triturus helveticus*. Subvertebral flexures are lacking, the amount of musculature is reduced, and the *transversus* originates along the ventrolateral edges of the centra. This is almost precisely the situation seen in lizards (see Fig. 97), even though the latter are procoelous. This may indicate that the exact position of the ball-and-socket joint (procoelous or opisthocoelous) is not critical. What matters is the sort of musculature present when it was necessary to strengthen the intercentral joint. *Siren* (Fig. 97) exhibits a pattern that is almost certainly derived from that seen in newts. A false anterior basapophyseal muscle has been developed from muscle fibers attaching along the front of each anterior lamella. However, the *subvertebralis* is otherwise simple and the *transversus* originates along the lateral edges of the centra and ventral lamellae. The vertebral column of *Siren* is cushioned in a large amount of axial musculature, which is, however, of simple structure.

B. Phylogenetic Reconstruction

i) Introduction

In this section the phylogenetic relationships of the families of salamanders are discussed and reasons put forth to support the proposed phylogeny. Each family is considered in turn, previous theories of relationship discussed, and conclusions reached. Intra-familial phylogenies are reconstructed, usually by means of cladograms. This is not done because of acceptance of cladistic principles of classification (see above), but because cladistic representation is the most reasonable when dealing with organisms from a single time (the Recent). Cladistic representation failed, however, when it came to diagramming the familial phylogeny of the entire Caudata. In this case a standard phylogenetic reconstruction was used.

I have attempted to make use of evidence from as many sources as possible, considering the negative as well as the positive data. After the relationships of each family to the other families have been discussed, a phylogenetic reconstruction for the Caudata is proposed and this is translated into a new classification.

ii) Hynobiidae Cope 1860

CONTENT. *Hynobius* Tschudi 1838, *Pachypalaminus* Thompson 1912, *Batrachuperus* Boulenger 1878, *Ranodon* Kessler 1866, *Onychodactylus* Tschudi 1838, ?*Wolterstorffiella* Herre 1939, ?*Bargmannia* Herre 1955, ?*Geyeriella* Herre 1950.

FOSSIL RECORD. *Wolterstorffiella*, from the Paleocene of Europe, and *Bargmannia*, from the Miocene of Europe, were referred to the

Ambystomatidae by Herre (1950, 1955). *Geyeriella*, from the Paleocene of Europe, was believed to be a plethodontid (Herre 1950), but the well-developed anterior basapophyses forbid such an assignment, as noted by Estes (1965b). *Geyeriella* is very similar to *Bargmannia* in the structure of the trunk vertebrae and is surely referable to the same family, whatever that might turn out to be.

Estes (1965b) suggested that *Geyeriella* and *Bargmannia* were best placed in the Ambystomatidae, but from the published figures and descriptions they fit equally well within the Hynobiidae. The elongate vertebrae with extremely robust anterior basapophyses may indicate an elongate, paedogenic salamander. It would be necessary to know the patterns of spinal nerve exits in order to make an exact familial determination. The cranial fragment of *Bargmannia* figured by Herre (1955, fig. 5) possesses a separate prootic with a well-developed anterolateral boss. This boss is a hynobiid-like feature, serving for support of the pterygoid. Also, the separate prootic, although retained in dicamptodontines, is a basic hynobiid feature. I suggest tentatively that these two genera represent early derivatives from a hynobiid stock and that they be classified within the Hynobiidae. Based on the close resemblances of the vertebrae, it is possible that the two are congeneric.

Auffenberg and Goin (1959) suggested that *Wolterstorfiella* was a hynobiid, whereas Estes (1965b) preferred to classify it as an ambystomatid. Although the rib-bearers are bicipital, they are closely appressed, as in hynobiids. As noted by Tihen (1958) and Holman (1968), the vertebrae of these two families are very similar, although the

rib-bearers tend to be more closely appressed in hynobiids. In this feature, the form of the hyperapophyses, and general proportions, the vertebrae of *Wolterstorffiella* are most similar to those of hynobiids (compare Figs. 2 and 3 with Kuhn 1962, fig. 15). Therefore, on the available evidence, I provisionally classify this genus in the Hynobiidae.

If these re-classifications prove valid, the range of the Hynobiidae is extended into the Paleocene of Europe. Further study of these most interesting specimens is urgently needed to clarify their taxonomic position and to test the ideas here advanced. Except for these taxa, hynobiids are not yet known from the fossil record.

RELATIONSHIPS. The Hynobiidae were not at first recognised as a separate taxon, and the species were lumped with the Ambystomatidae (see above). It has, however, been long recognised that hynobiids are the most primitive of living salamanders (Dunn 1922, Noble 1931), being at least structurally ancestral to the other living groups. On the basis of in-group (within the Caudata) and ex-group comparisons, the following character states are considered to be primitive:

1. Premaxillae paired with short facial spines.
2. Lacrimal and septomaxillary bones retained.
2. Angular and prearticular separate in the lower jaw.
4. Columella and operculum both present in the middle ear.
5. Fertilization external.
6. Second epibranchials retained in the hyobranchium of metamorphosed individuals.

Although Dunn (1922) considered *Tylotriton* to possess the most

primitive cranial anatomy among all salamanders, it is all but certain that the structure seen in hynobiids is a far closer approximation to the true ancestral condition. *Tylototriton* has a superficially archaic skull, but this "primitiveness" breaks down upon closer examination (see below).

I would add the following features to the above, previously accepted, list:

1. *Subvertebralis* with anterior basapophyseal musculature and associated transverse process (= posterior) flexures.
2. *Dorsalis trunci* with relatively long anterior flexures.
3. *Rectus abdominis* divided into two distinct units: the *rectus abdominis superficialis* and the free *r. a. profundus*, which connects the hyobranchium and the pelvis.
4. Only two layers of lateral abdominal musculature: the *obliquus externus (superficialis)* and *transversus*, the *o. e. profundus* and *o. internus* being absent in most metamorphosed adults.
5. Spinal nerves with intervertebral exits, except in the case of those associated with the atlas (see Edwards 1976).
6. Vertebrae relatively long and low, with amphicoelous centra and appressed rib-bearers.

The characters suggested as primitive for the Hynobiidae were chosen on the bases of several criteria. Hynobiid cranial structure is determined to be primitive on the basis of ex-group comparisons, especially with frogs and dissorophids (see Bolt 1969, Eaton 1973), thus forming one end of the morphocline. External fertilization is

also primitive owing to ex-group comparisons. As regards trunk musculature, the suggested primitive states are mainly arrived at by correlating transformation series and on the basis of ontogenetic data. Other, more derived families, can be derived from hynobiids by means of paedomorphosis of the trunk musculature. It is, of course, possible that rather than being truly primitive for the Caudata certain of these features are divergently specialized. Nevertheless, it is evident that, in principle, hynobiids represent a structural grade from which the other families are derivable. While recognizing the realities of mosaic evolution and continued change in "primitive" lineages, hynobiids are here accepted as the most primitive living salamanders and truly ancestral salamanders, if known, would probably be classified in the Hynobiidae.

Unfortunately little work has been done on the relationships of the hynobiid genera and species, with Dunn's (1923a) excellent monograph remaining the first and only adequate study. Dunn considered *Hynobius* to be the "central" hynobiid from which the other genera were derived. He also attempted to relate the other hynobiid genera with individual species of *Hynobius*. The monotypic *Pachypalaminus* was suggested to be closely allied to *Hynobius vandenburghi* (= *H. nebulosus* at present) and it is sometimes classified as a member of *Hynobius* (see Thorn 1968). Dunn allied *Batrachuperus* to *H. keyserlingii*, while *Ranodon* and *Onychodactylus* were also derived from *Hynobius*. Noble (1931) followed Dunn in considering *Hynobius* as the most primitive and the other genera directly derived from it.

As noted by Noble (1931) and unfortunately still true, the life habits of hynobiids are very little known. As well, the functional

significance of most of the character states are not known. This is especially true as regards cranial osteology, which differs significantly from that of most other salamanders. Systematic revision of the family is needed, as well as detailed functional studies.

iii) Cryptobranchidae Cope 1889

CONTENT. *Cryptobranchus* Leuckart 1821.

FOSSIL RECORD. As noted below, I recognize only one genus of cryptobranchid salamanders, thereby including the fossil species assigned to *Andrias* in the genus *Cryptobranchus*.

Meszoely (1967) named a new genus and species of salamander from the Eocene of Wyoming as *Piceoerpeton willwoodense*, which was based on a single fragmentary trunk vertebra. Although he assigned it to the Cryptobranchidae, Estes (1969a) later suggested that it was a member of the extinct family Scapherpetontidae. Extensive material referable to *Piceoerpeton* has been collected from the Paleocene of southern Saskatchewan (Ravenscrag Formation), including atlantes and trunk vertebrae. However, two distinct sorts of jaws are potentially referable to this material. Depending upon which elements belong with the vertebrae, *Piceoerpeton* could be the earliest known cryptobranchid or, more probably, a batrachosauroidid (Naylor and Krause, in prep.).

The other fossil cryptobranchids have been traditionally placed in the genus *Andrias* Tschudi 1837 (see Westphal 1958, Meszoely 1966), but considering the genus group in other families of the Caudata shows this usage to be unjustified. As shown elsewhere (Naylor 1978c), I believe *Andrias* to be properly a junior synonym of *Cryptobranchus*.

Tschudi (1837) described the first recognized fossil cryptobranchid as *Andrias scheuchzeri*. As noted by Westphal (1958), Holl (1831) had previously named the type specimen *Salamandra scheuchzeri*, making the proper designation *Cryptobranchus scheuchzeri* (Holl). *C. scheuchzeri* is known from the Oligocene, Miocene, and Pliocene of Europe (see Thenius 1954, Westphal 1958, 1967, 1970). North American cryptobranchid fossils from the Miocene and Pliocene are probably from a single species, *Cryptobranchus matthewi* (Cook), as shown by Meszoely (1966). These specimens have also been reported on by Cook (1917), and Tihen and Chantell (1963). *C. japonicus* is known from the Pleistocene of Japan (Shikama and Hasegawa 1962), and *C. alleganiensis* comes from the subrecent of North America (Nickerson and Mays 1973).

RELATIONSHIPS. There are probably three living species of *Cryptobranchus*: *C. alleganiensis* from eastern North America, *C. japonicus* from Japan, and *C. davidianus* from China. *C. alleganiensis* is paedomorphic in comparison to the other species, but has a similar ecological role and the structure is very similar.

Cryptobranchids differ from hynobiids in their larger size, flattening and increased ossification of the skull, the loss of the septomaxillary and lacrimal bones from the snout, and the retention of various larval features (see Noble 1931). They resemble hynobiids in retention of external fertilization, separation of angular and prearticular in the lower jaw, basic structure of the vertebrae (see Fig. 3) and trunk musculature (compare Figs. 25 and 27), and basic structure of the carpus and tarsus (see Schaeffer 1941). Dunn (1922, 1923a) recognized the close resemblance to hynobiids, noting that

cryptobranchids were directly derived from the former. Noble (1931) and all subsequent workers have retained this concept, generally accepting Dunn's (1922) classification of the two families in the Cryptobranchioidea (but see Regal 1966) and this scheme is here followed.

Relationships of the known species of Cryptobranchidae are uncertain. Based on the structure of the hyobranchia (see Edgeworth 1923, Fukuda 1928), and the presence of open gill slits in adult *C. alleganiensis*, the North American species is probably a paedomorphic derivative of the species previously called *Andrias*. Meszoely (1966) showed that *C. matthewi* is probably closer to *C. japonicus* than to *C. alleganiensis*, and Westphal (1958) pointed out the close resemblance of *C. scheuchzeri* to *C. japonicus*, classifying them as a single species. As noted above, the proper assignment of *Piceoerpeton* is uncertain.

iv) Schapherpetontidae Auffenberg and Goin 1959

CONTENT. *Scapherpeton tectum* Cope 1876, *Lisserpeton bairdi* Estes 1965.

RELATIONSHIPS AND OCCURRENCES. In 1876 Cope named a new genus of fossil salamander from the Judith River Formation, Montana. In *Scapherpeton*: "Vertebrae [are] deeply biconcave, with opposed, but not continuous, foramina for the chorda dorsalis Centrum with vertically compressed, short diapophyses near the posterior extremity, a prominent hypapophyseal keel, and prolonged neural spine [= hyperapophysis]" (Cope 1876, pp. 353-354). Cope recognized four species of

this genus, and also erected another genus and species, *Hemitrypus jordanus*, from the same formation.

Utilizing additional material from the Hell Creek, Lance, and Judith River (including the Oldman of Alberta) formations, Auffenberg and Goin (1959) synonymized the named species of Cope with *Scapherpeton tectum*. They assigned an atlas to this species, which Estes (1964) showed subsequently to be referable to *Opisthotriton*. In addition, they erected a new family Scapherpetonidae (emended to Scapherpetontidae, see Kuhn 1967, Estes 1969a), which was compared to amphiumids and cryptobranchids, but with no explicit statement as to possible relationships provided.

Auffenberg and Goin (1959) discussed *Hemitrypus jordanus* and referred additional material to the species (based on a broken trunk vertebra), noting (p. 8) that it differed from "*Scapherpeton* in lacking a strong midventral keel" and in the possible presence of anterior basapophyses. The possibility of synonymy was discussed but rejected as, if the two sorts of vertebrae came from a single species, it was considered that the resulting "variation along the column is more than would normally be expected on the basis of modern urodeles" (p. 10).

In his monograph on the lower vertebrates from the Lance Formation, Estes (1964) provided extensive description of *Scapherpeton*. He referred numerous elements to the vertebral material (upon which *S. tectum* is based): dentaries, maxillae, premaxillae, exoccipitals, parietals, and limb elements. Except for the perhaps problematical limb elements, Estes' associations are probably correct, as confirmed

by subsequent discoveries in other localities. The other salamanders known from the Lance (and other formations) are well associated: *Opisthotriton* is known from articulated skeletons, including a complete specimen from Alberta (see also Estes 1975); *Habrosaurus* shows clear sirenid features; and the associations of cranial material with *Prodesmodon* are now understood (Naylor 1978a).

Estes (1964) classified the Scapherpetontidae in the Cryptobranchioidea: "The vertebrae of *Scapherpeton* are of simple type if the development of the prominent ventral keel is ignored. The simple, double-headed rib-bearers, general lack of strong muscular ridges or crests, long, slender neural spines [= hyperapophyses], and amphicoelous vertebrae probably are indicative of a relatively primitive organization" (p. 66). The distinctly bicipital rib-bearers and long hyperapophyses of *Scapherpeton* are not, however, to be expected in a cryptobranchoid, nor is amphicoely or lack of muscle crests necessarily primitive.

Estes (1964) noted that the vomers are like those of *Cryptobranchus*, and there are resemblances in the "depressed form" and short nasal spines of the premaxillae. The general shape and surface for articulation with the squamosal on the parietal are also like those of *Cryptobranchus*. The exoccipitals resemble those of cryptobranchids in general shape, the "swept-back condyles," and the large vagal and tiny hypoglossal foramina. They differ in having a large dorsal suture for articulation with the parietals (see Estes 1964 for descriptions). As regards the vertebrae, Estes (1964) held that the long hyperapophyses and position of the transverse processes were cryptobranchid-like,

and that the high neural arch and hatchet-shaped neural crest were similar. He also argued that the femoral head resembled that of *Cryptobranchus*.

Estes (1965a) subsequently named and described another genus and species of scapherpetontid, *Lisserpeton bairdi*, from the Upper Cretaceous Hell Creek Formation, Montana, which was based on a trunk vertebra very similar to those of *Scapherpeton*. He noted its occurrence in the Lance Formation of Wyoming and in the upper Paleocene of Wyoming and Montana. The vertebrae were held to differ from those of *Scapherpeton* in the following features: no "ossification" within the cotyles, cotyles more rounded, vertebrae generally less robust, deep subcentral fossae, dorsal arm of rib-bearer arising from the dorsal surface of the wall of the neural arch, and well-developed zygapophyseal ridges. Atlantes (with no constriction at the base of the odontoid process), parietals, maxillae (with fewer teeth than in *Scapherpeton* and the *pars facialis* further posterior), and a vomer were referred to the species. Estes (1976) subsequently referred dentaries to *Lisserpeton* from the Paleocene of Montana.

Estes (1965b, 1969a) later reinterpreted the relationships of scapherpetontids. He noted discovery of postdentary bones referable to *Scapherpeton* in which the angular and prearticular were fused, and that the maxillae were not cryptobranchid-like in structure. These facts indicate ambystomatid (especially larval *Dicamptodon*) rather than cryptobranchid relationship as do the widely bicipital rib-bearers. At present (Estes 1969a, 1976, but see Edwards 1976) the Scapherpetontidae are classified in the Ambystomatoidea, with

ambystomatids, plethodontids, and batrachosauroidids. Estes (1969a, p. 231) believed scapherpetontids to be close to the Batrachosauroididae, primarily on the basis of the common possession of large vertebrarterial fossae, long and robust hyperapophyses, and "general form of the centrum and neural arch." He also argued that the double canals at the base of the broken rib-bearers in Meszoely's figure (1967, fig. 1) of the type specimen of *Piceoerpeton* indicated widely separated rib-bearers, which is confirmed by the Ravenscrag material. This plus the large anterior vertebrarterial fossa, deeply amphicoelous cotyles, and robust hyperapophysis, were held to indicate that *Piceoerpeton* was a derivative of *Lisserpeton*. As noted above, referral of jaw material to the vertebrae called *Piceoerpeton* is uncertain, and the relationships of the genus remain unknown.

Estes (1975, 1976) reported *Scapherpeton* from the upper Paleocene Fort Union Formation of Wyoming and the middle Paleocene Tongue River Formation of Montana. Material from the latter formation was also referred to *Lisserpeton*, the dentaries of which have non-pedicellate teeth and resemble those of batrachosauroidids. Estes (1976) suggested that this supported the previously hypothesized relationship of scapherpetontids to the batrachosauroidids. *Scapherpeton* is also known from the Ravenscrag Formation in Saskatchewan (Naylor, in prep.).

Most recently, Edwards (1976) has reclassified *Scapherpeton* and *Lisserpeton* in a new family Dicamptodontidae, along with *Dicamptodon* and *Rhyacotriton*. This was done on the basis of the patterns of the exits of spinal nerves and the supposed similarity in vertebral structure between *Scapherpeton* and *Dicamptodon*. Although the patterns

of spinal nerve foramina along the column are conformable in the four genera, this is the only detailed resemblance among them. Further, *Amphiiuma* has a similar sort of pattern (see Edwards 1976). The common possession of the spinal nerve pattern is equally (or more) probably a reflection of derivation from a stock intermediate between cryptobranchoids and ambystomatines. As such, it does not necessarily indicate special relationship of scapherpetontids and dicamptodontines and, at present, it is preferable to retain the family Scapherpetontidae.

Based on the pattern of spinal nerve exits, probable presence of anterior basapophyses and correlated anterior basapophyseal musculature, fused postdentary bones, divergently bicipital rib-bearers, and long hyperapophyses, I classify the Scapherpetontidae as a separate family within the superfamily Ambystomatoidea along with the Amphiumidae and the Ambystomatidae. The cryptobranchid resemblances noted by Estes (1964) indicate relatively early divergence from the basal ambystomatoid stock, but the sequence of splitting of scapherpetontids and amphiumids (see below) is uncertain. It is probable that amphiumids share a similar, but separate, ancestry within this basal stock, thus justifying classification in the same superfamily on the principles of evolutionary systematics (see above).

v) Amphiumidae Gray 1825

CONTENT. *Proamphiiuma* Estes 1969, *Amphiiuma* Garden 1821.

FOSSIL RECORD. Estes (1969b) has named and described the earliest known amphiumids as *Proamphiiuma cretacea*, from the Upper Cretaceous of Montana, and *Amphiiuma jepsoni*, from the Paleocene of Wyoming.

Proamphiura is also known from the Oldman (= Judith River) Formation of Alberta (Fox 1976), and the Fruitland Formation of New Mexico (J.G. Armstrong, pers. comm.).

As noted by Estes (1969b), the atlantes and trunk vertebrae of *Proamphiura* are distinctly amphiumid, leaving no doubt as to their proper familial assignment. In comparison to those of living *Amphiura*, the vertebrae are less extremely modified. They are somewhat elongate and delicate, with less development of the crests and processes diagnostic of *Amphiura*, presumably indicating greater similarity to more primitive urodeles. The atlas, however, is very like that of *Amphiura*, presumably owing to attainment of similar cranio-atlantal relationships and associated musculature (see Estes 1969b, fig. 1, also Fig. 4). Estes (1969b, p. 5) states that "*Proamphiura* is structurally an ancestor of *Amphiura* and there is no impediment to considering it a real ancestor, as well," which is a reasonable conclusion.

A single left dentary (UA 14316, Fig. 98) from Bug Creek Anthills, Hell Creek Formation, Montana is now referable to *Proamphiura*. It is quite small (ca. 6.5 mm long) and of a size conformable with that expected from the known vertebrae and atlantes (collections of The University of Alberta, see also Estes 1969b). The symphseal region and part of the rear is broken off, but most of the tooth row is apparently present. The jaw is not referable to any salamander previously described from the Hell Creek or other Upper Cretaceous localities and in overall shape it is similar to dentaries of *Amphiura* means.

The tooth-bearing flange is relatively deep and there are relatively few teeth, each being large, which are features of *Amphiura*. Although the pedicles are all broken, positions and approximate sizes of the teeth are clearly evident from the ridges remaining. These ridges are similar to those left in Recent *Amphiura* when tooth pedicles are broken from the dentary. An internal, horizontal shelf below the tooth row presumably held the developing replacement series. This differs somewhat from that of *Amphiura*, in which the lower part of the dentary itself holds the replacement series. The area for the articulation of the postdentary bone is similar to that of *Amphiura*, with the development of dorsal and ventral flanges for acceptance of the forward projection of the postdentary. *Proamphiura* differs in lacking a distinctly raised portion of the dorsal flange, although there is a raised surface in the same position. Finally, the specimen has distinct external mental foramina, as in *Amphiura*.

Amphiura jepsoni is probably closely related to the living *Amphiura*. According to Estes (1969b), the crests and keels of the vertebrae are more accentuated than is the case in *Proamphiura*. The partial skull is noteworthy in its combination of relatively primitive (wide snout, disposition of the vomers and vomerine teeth, relatively broad parasphenoid, and relatively short maxillae, see Estes [1969b]) and derived (single premaxilla, elongate premaxillary spine, apparent loss of lacrimals and septomaxillae, dorsal concavity of the articular surface of the quadrate, and frontal surrounding the olfactory tracts, see Estes [1969b]) features. The primitive features probably correlate with the retention of a relatively broad head. The vomers are more

larval and less derived than those of living *Amphiurna*. That is, the posteriorly elongate, longitudinal vomerine tooth series of *A. means* is not owing to neoteny (compare salamandrids), but to the narrowness of the skull. This interpretation is supported by the lack of participation of the pterygoid in the palatal tooth rows and by the absence of palatine teeth.

The structure of the quadrate, with the dorsally concave articular surface, and of the "prominent fossa for adductor muscle attachment . . . [and of the] blunt coronoid process" on the lower jaw (Estes 1969b, p. 9) indicate attainment of the cranial musculature and mechanics seen in living *Amphiurna*, even though the skull is much broader. This inference is supported by the structure of the atlas already present in the Cretaceous *Proamphiurna*.

The known amphiurid fossils can say little of the ultimate origins of the family. They are valuable in providing times and places of occurrence, thus providing minimum ages for the origination of the family. Nevertheless, the evidence allowing for the drawing of phylogenetic conclusions must come from study of living species in this case.

RELATIONSHIPS. Cope (1889) placed *Amphiurna* in a separate suborder, which he believed to be derived from desmognathines and, in turn, to be ancestral to apodans. There are resemblances between *Desmognathus* and *Amphiurna* in the structure of the posterior part of the skull, atlas, and certain aspects of the associated musculature, but as there are marked differences in other respects these resemblances are probably owing to convergence. Reed (1920), basing his interpretation on the

auditory region, suggested a relationship to plethodontids (as did Dunn [1922, 1926]) and classified the family with plethodontids, salamandrids, and ambystomatids in the Salamandroidea. By contrast, Noble (1931) believed *Amphiuma* to have come from a salamandrid stock, while Herre (1935b) suggested a specific ancestor shared with the newts *Euproctus* and *Pachytriton*. Larsen (1963), basically using data from the cranium, also favoured a relationship with salamandrids.

Regal (1966, p. 404) separated the Amphiumidae from the Salamandroidea, placing it alone in the Amphiumoidea, "in the anticipation that future studies will demonstrate relationships to the plethodontid-ambystomatid section of the Ambystomatoidea." On the basis of enzyme analysis, Salthe and Kaplan (1966) claimed *Amphiuma* to be very close to plethodontids, with origin of this lineage in the Triassic and of *Amphiuma* from the plethodontids in the Cretaceous. This interpretation is at variance with the anatomical evidence and can be rejected. On the basis of patterns of courtship, Salthe (1967) also claimed a plethodontid relationship, but study of his data indicates that, in fact, courtship patterns are quite different between *Amphiuma* and plethodontids. Basically on spinal nerve exits Edwards (1976) derived amphiumids from a stock that led ultimately to ambystomatids, plethodontids, and salamandrids.

Elucidation of the relationships of amphiumids is difficult. It is easier to refute previous hypotheses (i.e., those of special plethodontid or salamandrid relationship) than it is to produce counterproposals. *Amphiuma* exhibits traits that generally seem to be unique specializations (autapomorphies) on a basically primitive

structural plan. Evidence from Edwards' (1976) study of the patterns of spinal nerve exits and comparison of the trunk musculature of amphiumids and plethodontids prohibits any close relationship of these two families. The same holds true for the hypothesis of salamandrid relationship, but to an even greater degree.

The number of chromosomes ($2n=28$, see Morescalchi 1975) of *Amphiuma* is shared with ambystomatids, excluding *Rhyacotriton*. The pattern of the exits of spinal nerves is similar, although not identical, to that of dicamptodontines and scapherpetontids. Cranial structure is advanced well beyond the hynobiid stage (Reed 1920, Larsen 1963), as is the presence of internal fertilization by cloacal apposition (Salthe 1967).

The trunk musculature is highly modified, but derivable from that seen in ambystomatids. The *dorsalis trunci* and *subvertebralis*, although altered by the accentuation of certain flexures and the development of new ones (see Figs. 28, 29, and 30), is of the basic pattern seen in hynobiids and ambystomatids, but very different from that of any plethodontid or salamandrid. Of special note is the structure of the lateral abdominal musculature. The relationships and pattern of each of its components (excepting the *transversus*) are identical to the situation in *Rhyacotriton*, and very similar to that of *Dicamptodon*. This is most suggestive, as it correlates with the exits of the spinal nerves discussed by Edwards (1976).

These resemblances strongly suggest affinity with the Ambystomatoidea (excluding the Plethodontidae), but the precise phylogenetic relationships remain obscure. The following are probably the more reasonable hypotheses:

1. Amphiumids are an early, independent branch from ambystomatid ancestry, represented by *Dicamptodon* and *Rhyacotriton*. Therefore, under evolutionary principles, they are to be classified as a separate family within the Ambystomatoidea along with ambystomatids and scapherpetontids.

2. *Amphiuma*, *Dicamptodon*, *Rhyacotriton*, and possibly scapherpetontids are a monophyletic assemblage and should, therefore, be classified in a separate family or superfamily.

3. Amphiumids and scapherpetontids may share a common ancestor, but the positive support for this is slight.

At present the first possibility appears to be the most reasonable. Amphiumids are in some ways intermediate between hynobiids and ambystomatids, being most like the more primitive members of the latter. *Amphiuma* shares derived features with ambystomatids in general (elongate premaxillary spine[s], internal fertilization, and number of chromosomes) and with dicamptodontines in particular (similar patterns of spinal nerve exits and lateral abdominal musculature). Its other features (single element in the middle ear, longitudinal vomerine tooth rows, fused premaxilla, complex *dorsalis trunci* and *subvertebralis*, structure of the atlas and trunk vertebrae, ossified hyobranchium, and general structure of the skull) are independently derived. Therefore, the Amphiumidae are to be classified with the Ambystomatidae and Scapherpetontidae in the superfamily Ambystomatoidea.

vi) Ambystomatidae Hallowell 1857

CONTENT. *Ambystoma* Tschudi 1838, *Rhyacosiredon* Dunn 1928, *Rhyacotriton* Dunn 1920, *Dicamptodon* Strauch 1870, ?*Ambystomichnus* Peabody 1954.

See Table 1 and Tihen (1958) for classification and content of species groups within *Ambystoma*.

FOSSIL RECORD. As is generally true for salamanders, the record of ambystomatids is sparse. *Ambystomichnus montanensis*, from Paleocene trackways in Montana, is probably related to *Dicamptodon* and may represent the earliest known ambystomatid (Peabody 1959, Tihen 1958).

Estes (1965b) notes an elongate ambystomatid from the Eocene of North Dakota, but this specimen has never been described. The presumed fossil ambystomatids from the Tertiary of Europe (*Wolterstorffiella*, *Geyeriella*, and *Bargmannia*) are discussed above, where it is concluded that they are probably hynobiids, which limits the fossil record of the Ambystomatidae to North America. Occurrences of *Dicamptodon* and *Ambystoma* are discussed above under the descriptions of the trunk musculature.

The fossil record is of little direct relevance to elucidation of the inter- and intrafamilial relationships of the Ambystomatidae.

RELATIONSHIPS. Tihen (1958), in a comprehensive study of the osteology of the Ambystomatidae, divided the family into three subfamilies: Dicamptodontinae, Rhyacotritoninae, and Ambystomatinae. The Dicamptodontinae included only *Dicamptodon* and the Paleocene *Ambystomichnus*, which is based on trackways. *Dicamptodon* retains a lacrimal and the primitive division of the otic region into exoccipital and prootic bones. The premaxillary spines are broad, but this is evidently a secondary phenomenon, as larval *D. ensatus* have narrow, elongated spines. The pterygoids have extended anteriorly to abut

against the maxillae in metamorphosed individuals. The Rhyacotritoninae held only *Rhyacotriton*, a monotypic genus from western North America. It differs from *Dicamptodon* in lacking a nasal (although the lacrimal is retained), having narrow premaxillary spines, and in having greatly reduced lungs. Tihen (1958) believed these two subfamilies to be early, independent branchings from ambystomatid stock.

Tihen's Ambystomatinae contains two genera, *Rhyacosiredon* and *Ambystoma*, the latter divided into subgenera and species groups as follows:

Genus *Ambystoma*

Subgenus *Ambystoma*

A. mexicanum species group

A. tigrinum species group

A. opacum species group

A. maculatum species group

Subgenus *Linguaelapsus*

(*A. cingulatum* and allies)

Subgenus *Bathysiredon*

(*A. dumerilii*)

A. tigrinum and its allies were considered to be the more primitive members of the genus, with the genus *Rhyacosiredon*, the *A. mexicanum* group, the subgenus *Bathysiredon*, and the *A. maculatum* group and its allies being derived from this stock. The *A. maculatum* species group and its allies (subgenus *Linguaelapsus* and the *A. opacum* group) were believed to be the most derived members of the genus.

As discussed above, Edwards (1976) created a new family Dicamptodontidae for *Dicamptodon*, *Rhyacotriton*, *Scapherpeton*, and

Lisserpeton. These genera seem to share a unique pattern of spinal nerve exits: postatlantal trunk nerves are intervertebral, whereas the postsacral nerves are intravertebral. However, the taxonomic weight of this character is problematical, and basing a classification on a single character is not without problems. It is presently preferable to retain the traditional families.

Nevertheless, Edwards' (1976) work on spinal nerves is suggestive as regards the relationships of *Dicamptodon* and *Rhyacotriton*. As the trunk musculature of the two genera is similar in presumably derived features (see Figs. 33, 34, and 35), the spinal nerves provide additional information suggesting affinity. Regal (1966) also argued that *Dicamptodon* and *Rhyacotriton* should be classified together, including them in the Dicamptodontinae. In addition to the presumedly derived features, they share several primitive features (retention of lacrimal and separate exoccipital and prootic). These shared features are sufficient to justify their inclusion in the subfamily Dicamptodontinae, which is the most primitive of the family Ambystomatidae.

Tihen (1958) suggested that *A. tigrinum* and its allies were the most primitive living *Ambystoma*. This was based on their possession of the following features:

1. "The absence of specializations found in members of the other groups" (pp. 33-34).
2. Vomer with a postdentigerous process.
3. Premaxillary spines short and broad in comparison to those of the other groups.
4. Palatine teeth always present.
5. *Os triangulare* subequally triradiate.

In contrast to Tihen's interpretations, based on osteological features, I regard the *A. tigrinum* group as derived. In comparison to hynobiids, *A. tigrinum* is decidedly more apomorphic than are members of the *A. maculatum* and *A. opacum* species groups. The so-called lack of specializations in *A. tigrinum* is, in fact, a reflection of derived simplification by means of paedomorphosis.

Vertebrae of *A. tigrinum* are short and high, with short, distinctly bicipital transverse processes, features that are larval (see Fig. 9). If the vertebrae of adult *A. maculatum*, *A. jeffersonianum*, *A. macrodactylum*, and *A. gracile* are compared with vertebrae from hynobiids (see Figs. 2, 3, 6, 7), the resemblances are readily apparent. These vertebrae are elongate, relatively low, and have long, more or less closely appressed rib-bearers. The vertebrae of adult *A. tigrinum* resemble those of larval members of the *A. maculatum* group. On the basis of in-group and ex-group comparison of vertebrae, *A. tigrinum* is most derived.

This relationship is even more evident in the trunk musculature. *A. tigrinum* possesses the full complement of *obliquus externus superficialis*, *o. e. profundus*, *o. internus*, and *transversus* in the lateral abdominal series. These muscle layers are found in larval members of the *A. maculatum* group, but adults lack the *o. internus*. The *rectus abdominis* of adult *A. tigrinum* is a single, simple band of muscle fibers extending anteroposteriorly, as is found in larval salamanders generally. Adults of the *A. maculatum* group, however, have a double *rectus abdominis* divided into a superficial and a deep portion. This double *rectus* and the lack of an *o. internus* is also seen in hynobiids

(although the paedomorphic *Onychodactylus* differs), indicating the primitive nature of *A. maculatum* and its allies.

Tihen (1958) considered *Rhyacosiredon* to be an early, primitive derivative of *Ambystoma* or of a pro-*Ambystoma* stock. The partially ossified hyobranchium was held to be primitive and not owing to neoteny. The pointed teeth, "general form" of the pterygoid (said to be similar to that of the hynobiid *Batrachuperus*), possibly the low coronoid process on the prearticular, and possibly the ridge on the lingual surface of the dentary were all considered primitive. Dunn (1928), however, believed *Rhyacosiredon* to be a neotenic derivative related to *A. tigrinum* and this interpretation is the more reasonable.

Rhyacosiredon retains a larval vomer and pterygoid, as well as reduced numbers of maxillary teeth in the metamorphosed adult (see Tihen 1958). Although Tihen argued that ossification of the hyobranchium was primitive, consideration of the distribution of ossified hyobranchia throughout the Caudata does not permit this interpretation. Rather, it is seen as a derived response to the needs of a more aquatic life. Cryptobranchids, amphiumids, sirenids, and newts show ossification of the hyobranchium, seemingly in response to aquatic feeding (see also Özeti and Wake 1969, Wake and Özeti 1969). The other features presumed to be primitive by Tihen are equally, or more reasonably, explicable in terms of paedomorphosis. Furthermore, acceptance of the derived nature of *A. tigrinum* provides additional evidence against the primitive nature of *Rhyacosiredon*. This genus is best considered to be a late derivative from an *A. tigrinum*-like ancestor, and hence the most derived ambystomatid.

In light of recent work on members of the *A. tigrinum* group, the *A. mexicanum* group, and the subgenus *Bathysiredon* by Brandon (1970a,b, 1972, 1976, 1977) and previously known anatomical evidence, reinterpretation of these divisions is necessary. Brandon (1976) suggested that *A. dumerilii* (= *Bathysiredon*) be classified in the *A. tigrinum* group, and noted fertile hybrids between members of the *A. mexicanum* and *A. tigrinum* species complexes. He also pointed out difficulties in distinguishing members of the two groups. Throughout the remainder of this work the *A. tigrinum* group is used to also include those species placed by Tihen (1958) in *Bathysiredon* and the *A. mexicanum* group.

The remaining species groups (see Tihen 1958, also Table 1) contain the most primitive living species of *Ambystoma*. The structure of the vertebral column and trunk musculature (studied in *A. cingulatum*), as well as consideration of the data provided by Tihen (1958) and Krogh and Tanner (1972), indicate that recognition of a subgenus *Linguaelapsus* is unnecessary. This species complex will be referred to as the *A. cingulatum* species group.

The structure of the trunk musculature confirms Tihen's (1958) assignment of *A. opacum* and *A. talpoideum* to a single species group. Development of the *subvertebralis* and *dorsalis trunci* is almost identical and the lateral abdominal musculature is very similar (see Figs. 41 and 42). This controverts the suggestion of Krogh and Tanner (1972) that *A. talpoideum* is most closely related to *A. maculatum*. In fact, *A. opacum* and *A. talpoideum* are both derivable from the *A. maculatum* species group, but they are more similar to each other than

either is to members of the latter group. Based on the descriptions and figures of the hyobranchial apparatus and its associated musculature presented by Krogh and Tanner, there is no special resemblance of *A. talpoideum* to the *A. maculatum* group that is not also shared with *A. opacum*. The supposed resemblances seen by Krogh and Tanner may well be an artifact of cluster analysis of minor proportional differences.

There is the necessity for slight modification of Tihen's (1958) *A. maculatum* species group with respect to the species *A. macrodactylum* and *A. gracile*, which were included in it. These two species are to be removed from the *A. maculatum* group and placed in a separate unit, the *A. macrodactylum* species group. Resemblances between these two species groups are owing to the retention of characters primitive for the genus *Ambystoma*, and other facts argue for separation. Morescalchi (1975, p. 347) noted "differences in the morphology of the various pairs of homologous chromosomes . . . within the same group of species (e.g., between *maculatum* and *macrodactylum* of the group *maculatum*, subgenus *Ambystoma*)." Eaton (1933, 1934) argued that *A. macrodactylum* and *A. gracile* shared a streptostylic suspensorium with *Rhyacotriton*. Other authors have denied this, but although the presence of streptostyly is problematical there are nevertheless resemblances of the suspensorium in the three species (see Eaton 1933, fig. A). Additional evidence is presented under the anatomical descriptions of *A. macrodactylum* and *A. gracile*. The *A. macrodactylum* species group is in many ways the most primitive of living *Ambystoma* and it may be occupying the ancestral area where it arose from ancestors in common with the dicamptodontines.

Based on information gained from the trunk region and cranium, and reinterpretation of previously existing data, a modification of Tihen's (1958) reconstructed phylogeny is necessary. Although the usefulness of detailed phylogenetic interpretation at the species level is generally questionable, it is possible to suggest relationships at the species group level within the Ambystomatidae.

The subfamilies Dicamptodontinae and Ambystomatinae appear to share a sister-group relationship of descent from a common ancestor (see Fig. 99). Each has retained certain primitive features and modified others. The Ambystomatinae are primitive in the structure of the vertebrae and trunk musculature, as evidenced in the *A. maculatum* and *A. macrodactylum* groups. Dicamptodontines are derived via paedomorphosis in this regard, with high epaxial myomeres extending well beyond the ribs, and anterior flexures meeting medially with their internal surfaces shifted ventrally (compare Figs. 33, 34, 35, 36, and 39). The lateral abdominal musculature of dicamptodontines is distinctly larval, with a well-developed *rectus lateralis*, four layers in the lateral body wall, and a simplified *rectus abdominis* which is also derived in being folded laterally and dorsally over the *o. e. profundus*. Dicamptodontines are also derived in the narrow *o. e. superficialis*, which is not segmented by myocommata. By contrast, in the cranium, dicamptodontines are primitive and ambystomatines more derived (see Tihen 1958).

An early dichotomy between dicamptodontines and ambystomatines is probable, with the former having been isolated to the west of the Rocky Mountains. The ancestors of the family would seem to have been of

hynobiid stock (see Tihen 1958, and above), or at least from an ancestor represented structurally by living hynobiids. If Peabody (1954) has correctly referred the Montana Paleocene trackways called *Ambystomichnus* to a *Dicamptodon*-like salamander, this may date the primary ambystomatid dichotomy as a pre-Paleocene event.

After the dichotomy, the ambystomatines underwent their own divergence. Accepting that the *A. macrodactylum* and *A. maculatum* groups are the most primitive living ambystomatines, the subfamilial history becomes simpler and more reasonable than that proposed by Tihen (1958). *A. gracile* and *A. macrodactylum* are presumably primitive relicts in the western part of North America, with the species of the *A. maculatum* group having arisen from an ancestral stock that found its way into eastern North America. This interpretation is in closer agreement with the anatomical evidence and makes unnecessary Tihen's (1958) hypothesis that *A. gracile* and *A. macrodactylum* represent two separate invasions of the northwest from eastern North America. In this regard, studies of *A. tihenii* from the Oligocene of Saskatchewan indicate relationship to the *A. macrodactylum* group, not to the *A. opacum* group as suggested by Holman (1968).

The members of the *A. opacum* group are derivable from the *A. maculatum* group, as is the *A. cingulatum* group (Tihen 1958, Krogh and Tanner 1972). The exact sequence of splitting of these two derived stocks from the *A. maculatum* group is uncertain. As argued above, the *A. tigrinum* group also finds its origins in the *A. maculatum* group and, in its turn, probably gave rise to *Rhyacosiredon*. The Ambystomatinae can be divided into two subgroups: a plesiomorphic

section including the *A. macrodactylum*, *A. maculatum*, *A. opacum*, and *A. cingulatum* species groups, and an apomorphic section including the *A. tigrinum* species group and the genus *Rhyacosiredon*. This makes continued utilization of subgenera of *Ambystoma* unnecessary. Continued recognition of *Rhyacosiredon* follows from the principles of evolutionary taxonomy (explicitly rejecting the contentions of cladism) and from Darwin's (1859) principles of classification (see above). Hypothesized cladistic relationships are shown in Figure 99 and the classification chosen to reflect this is given in Table 1.

It may seem in some ways more reasonable to split the Ambystomatinae into two genera according to the division into plesiomorphic and apomorphic sections. The structural differences between the two units are relatively distinct and such a move would reflect cladistic and patristic relationships. Nevertheless, this would lead to numerous nomenclatorial problems. The genus *Ambystoma* is based on the species *A. maculatum*, which would necessitate naming the more primitive section *Ambystoma*. With the suppression of the generic names senior to *Ambystoma*, it would seem that the first available name for the apomorphic section would be *Axolotes* Owen 1844 (see Tihen 1969, p. 75.1), with the type species as *Axolotes mexicanum* (= *Ambystoma mexicanum*). Inclusion of *Rhyacosiredon* in this genus would be problematical. Such a major change would engender extreme confusion and it is doubtful that it would be accepted. In order to promote stability, it is best that the nomenclature remain as it is.

It is accepted that ambystomatids are derived from hynobiid or pro-hynobiid stock (Tihen 1958, Larsen 1963, Regal 1966) and closely

related to, or representative of, the actual ancestry of the Plethodontidae (Laurent 1947, Monath 1965, Regal 1966, Wake 1966). Ambystomatids share a common kind of trunk musculature with the Hynobiidae and are osteologically derivable from such ancestors. As argued above, they are related to the Amphiumidae and Scapherpetontidae, with which they are to be classified in the superfamily Ambystomatoidea. Basically on cranial evidence, close relationship of ambystomatids to plethodontids is well established (Regal 1966, Wake 1966). The character states shared by the two families are, however, basically of a primitive nature and, as argued below, I prefer to classify the Plethodontidae in their own suborder as they differ fundamentally in the structure of the trunk musculature.

Regal (1966) argued that *Rhyacotriton* could serve as a structural ancestor for the plethodontids, an hypothesis that finds support in the structure of the trunk musculature. *Rhyacotriton* has a simple, non-segmented *transversus* extending into the *subvertebralis*. Younger individuals of *Rhyacotriton* seem to lack the internal band of muscle fibers that extend anteromedially from the anterior basapophyseal septum. In older, larger individuals this layer is present. The smaller specimens have a condition very close to that of *Plethodon* and are structurally intermediate between the anterior basapophyseal and the posterior basapophyseal *subvertebralis*. In addition, the overlap of the *o. e. profundus* by a flap of the *rectus abdominis* resembles the plethodontid condition (compare Figs. 35 and 49). These resemblances, and the similarities of the auditory apparatuses (Larsen 1963, Monath 1965), are suggestive clues as to the origin of the Plethodontidae.

vii) Plethodontidae Gray 1850

CONTENT. *Plethodon* group: *Plethodon* Tschudi 1838, *Ensatina* Gray 1850, *Hemidactylium* Tschudi 1838, *Aneides* Baird 1849, ?*Batrachoseps* Bonaparte 1839; *Bolitoglossa* group: *Hydromantes* Gistel 1848, *Bolitoglossa* Duméril, Bibron, and Duméril 1854, *Lineatriton* Tanner 1950, *Thorius* Cope 1869, *Pseudoeurycea* Taylor 1944, *Chiropterotriton* Taylor 1944, *Oedipina* Keferstein 1868, *Parvimolge* Taylor 1941; *Eurycea* group: *Eurycea* Rafinesque 1822, *Gyrinophilus* Cope 1869, *Pseudotriton* Tschudi 1838, *Stereochilus* Cope 1869, *Haideotriton* Carr 1939, *Typhlotriton* Stejneger 1892, *Typhlomolge* Stejneger 1896; *Desmognathus* group: *Desmognathus* Baird 1850, *Leurognathus* Moore 1899, *Phaeognathus* Highton 1961.

FOSSIL RECORD. The record of plethodontids is sparse, consisting of a few trackways and several Pleistocene occurrences having little information on origins or intrafamilial relationships. Tihen (1968, p. 114) claims that fossils of *Plethodon* probably appear "before or during the Miocene," but the source of this is unknown to me. Peabody (1959) described lower Pliocene trackways from California referable to *Batrachoseps*, and Brame and Murray (1968) claimed these to belong to the extant *Batrachoseps relictus*. Vertebrae assigned to *Desmognathus* from the Pleistocene of Virginia (Gehlback 1965), *Plethodon glutinosus* from the Pleistocene of Florida (Holman 1958, 1959a,b), and *Pseudotriton ruber* from the Pleistocene of Georgia (Holman 1967) are also known.

RELATIONSHIPS. The phylogeny and classification of plethodontids have been a matter of dispute, although the situation has recently stabilized (Wake 1966). Unfortunately, the new information gained in this study and reinterpretation of previous data indicate the need for revision.

The first (and unsurpassed) detailed study of plethodontids, Dunn's (1926) *Salamanders of the Family Plethodontidae*, has had a lasting influence on concepts of relationship and it is now necessary to return to certain of Dunn's ideas. According to Dunn, plethodontids were derivable from salamandrids, except as regards the auditory apparatus. One of the major characters held to document the plethodontid-salamandrid relationship was the common occurrence of longitudinal rows of teeth along the palate. Noble (1931) noted resemblance between the "body musculature" of *Salamandra* and plethodontids, which has been confirmed by my study. However, Laurent (1947) demonstrated the basic dissimilarity of the vomerine and palatal teeth of plethodontids and the vomerine teeth of salamandrids. This evidence was accepted as justifying a change in classification, and plethodontids are now grouped with ambystomatids by most workers (Regal 1966, Wake 1966). This classification is based on features that are primitive for the Plethodontidae, but derived for the Ambystomatidae.

Regal (1966) suggested that *Rhyacotriton* is an acceptable structural ancestor for the plethodontids, as evidenced by the trunk musculature (discussed above) and similarities in development of the auditory structures (see Larsen 1963). Of course, certain autapomorphies prohibit the use of *Rhyacotriton* itself as a structural ancestor (i.e., loss of the nasal, loss of the *r. a. profundus*, chromosomal number of $n=13$).

The evidence from my study (see above), as well as data provided previously (Tihen 1958, Larsen 1963, Regal 1966, Wake 1966), indicates derivation of the Plethodontidae from a primitive ambystomatid or pro-ambystomatid. Shared similarities include: internal fertilization by means of a spermatophore, general configuration of the cranium, transverse vomerine tooth series (secondarily modified in plethodontids), patterns of the exits of spinal nerves (Edwards 1976), and general structure of the trunk musculature. Nevertheless, as argued under the Salamandridae below, I believe other information indicates that plethodontids should not be classified with the Ambystomatidae, but closer to the Salamandridae, with which they share basic adaptive trends. This is a return to the concepts of Dunn (1926) and Noble (1931), but for differing reasons and with differing details. It does not greatly affect the views of Regal (1966) and Wake (1966), but places different weights on certain characters.

Relationships within the Plethodontidae were first studied by Dunn (1926), who greatly influenced concepts of intergeneric relations up to the present. The work of Dunn was extremely detailed and well-reasoned, and I will argue for a return to certain of his ideas below. Since this time (Wilder and Dunn 1920, Dunn 1926) it has been accepted that plethodontids originated from ancestors inhabiting the mountain streams of Appalachia and reproducing aquatically (but see Salthe 1965, 1967, and below).

Dunn (1926) divided the Plethodontidae into desmognathines (*Desmognathus* and *Leurognathus*) and plethodontines as is presently accepted (Wake 1966), although without formal ranking. He separated

plethodontines into two generic groups (on the basis of the condition of the tongue): the *Plethodon* group having a fixed-tongue (*Plethodon*, *Ensatina*, *Hemidactylium*, *Aneides*, and *Batrachoseps*) and the free-tongued *Eurycea* group (*Eurycea*, *Gyrinophilus*, *Pseudotriton*, *Stereochilus*, *Typhlotriton*, *Typhlomolge*, *Hydromantes*, and "*Oedipus*"). *Gyrinophilus* was judged the most primitive living plethodontid, but he stated that *Plethodon* was also very primitive and derivable from no living genus.

In a phylogenetic reconstruction quite similar to that proposed below, Piatt (1935, p. 238, figure not numbered) suggested that the free-tongued species were diphyletic. "*Oedipus*" (= the supergenus *Bolitoglossa* of Wake 1966) and *Hydromantes* were judged to have been derived from an ancestor in common with the *Plethodon* group, while *Eurycea* and its allies were earlier independent derivatives. Piatt did not consider *Batrachoseps* to be as close to *Plethodon* as had Dunn.

By contrast, Tanner (1952), also basing his conclusions primarily on data from the hyobranchium and its associated musculature, united the free-tongued plethodontids as a monophyletic group. Wake's (1966) phylogeny of the Bolitoglossini is almost identical to that of Tanner, differing as regards the relationships of *Thorius* and *Hydromantes*. Wake removed *Hemidactylium* and *Batrachoseps* from Dunn's *Plethodon* group, placing them in the *Eurycea* group (renamed the Hemidactyliini) and with the neotropical free-tongued plethodontids (the Bolitoglossini), respectively. He considered *Hemidactylium* to be the most primitive living plethodontid, a conclusion controverted by my findings. Wake's (1966) phylogenetic reconstruction has the Hemidactyliini as the central plethodontid stock, with the Desmognathinae, Bolitoglossini, and Plethodontini branching sequentially from it.

More recently, Wake and Lombard (1973, p. 65) implicitly question this scheme, stating that "direct development only [evolved] once." This might seem to indicate that they consider bolitoglossines to have evolved from the Plethodontini, although later interpretations seem not in agreement (Lombard and Wake 1976).

I suggest a return to the basic concepts of Dunn (1926) and Piatt (1935), my classification being shown in Table 2. These changes from Wake's (1966) groupings involve taking *Hemidactylium* from the Hemidactyliini (to be called the Euryciini) and *Batrachoseps* from the Bolitoglossini, and placing them in the *Plethodon* group (tribe Plethodontini). My scheme differs from that of Dunn in considering the free tongue to have evolved twice.

Formal classification reflecting phylogeny (see Fig. 100, and below) necessitates recognition of two subfamilies: the Plethodontinae, with the tribes Plethodontini and Bolitoglossini; and the Desmognathinae, with the tribes Euryciini and Desmognathini. I am somewhat hesitant to suggest this step owing to the use of the subfamily Desmognathinae to contain only *Desmognathus* and its allies. Nevertheless, these formal groupings will be used here as they and the proposed phylogeny are in agreement with my studies on the trunk musculature, consistent with cranial osteology, more parsimonious with respect to biogeography, and (if the reinterpretation is accepted) consistent with life history data.

In terms of cranial anatomy, *Plethodon* is one of the most primitive of living plethodontids. Although Wake (1966) believed *Gyrinophilus* to be more primitive, my interpretation of his data and of the crania

indicates that they are probably equally primitive in this regard. The structural primitiveness of *Plethodon* is even more pronounced in the trunk musculature and hyobranchium (see Wake 1966, Piatt 1935, and above). The axial musculature of *Plethodon* is an almost perfect structural intermediate between the anterior basapophyseal musculature of primitive salamanders and the posterior basapophyseal sort of more derived plethodontids. In all apparent aspects, *Plethodon* is structurally ancestral to other plethodontids.

As noted by Dunn (1926), and corroborated by Wake (1966), *Ensatina* and *Aneides* are osteologically derivable from *Plethodon*. The detailed structure of the trunk musculature confirms this. The position of *Hemidactylium* has been uncertain: earlier workers (Dunn 1926, Noble 1931, Piatt 1935) derived it from *Plethodon*, but Wake (1966) indicated a closer alliance with the *Eurycea* group. Dunn (1926, p. 25) stated that *Hemidactylium* "has reverted to some extent to the still water breeding site of more primitive salamanders," and Noble (1931) supported this. Although Wake (1966) disagreed, believing the aquatic larval stage of *Hemidactylium* to be primitive, he provided no evidence to controvert Dunn's suggestions.

The eggs of *Hemidactylium* are laid amongst sphagnum moss along the edges of ponds, where they are attended by the female. Upon hatching, the young wriggle into the water where a short period (about six weeks) is spent prior to metamorphosis (Dunn 1926, Bishop 1943). The adult is terrestrial and avoids water. The filamentous gills of larval *Hemidactylium*, the possession of only three branchial bars, the position of egg deposition and the brooding female, the short larval

period, and the close structural resemblances between adult *Plethodon* and *Hemidactylium* all indicate the secondary nature of the latter's reproductive strategy. Lombard and Wake (1977) have shown resemblances in the tongue of *Hemidactylium* to that of *Plethodon* and its allies. Notably, the *genioglossus* of *Hemidactylium* is very like that of *Ensatina*, but differs from that of *Eurycea* and its relatives. The tongue of *Hemidactylium* is fixed as in all members of the *Plethodon* group, but unlike terrestrial euryciines. This reinterpretation does little violence to Wake's (1966) reconstruction, in which he noted that *Hemidactylium* was the most isolated "hemidactyliine." The genus fits much more readily into the Plethodontini.

The relationships of the bolitoglossines and of *Batrachoseps* have been uncertain. Dunn (1926) believed the free-tongued forms to be a natural group, as did Tanner (1952). Piatt (1935), however, argued that *Hydromantes* and "*Oedipus*" were not closely related to the eastern free-tongued plethodontids, but from *Plethodon* stock. Regarding the position of *Batrachoseps*, Dunn (1926), Noble (1931), and Tanner (1952) placed it with the *Plethodon* group (the Plethodontini), whereas Piatt (1935) argued that it was related to the bolitoglossines.

Wake (1966) separated *Hydromantes*, the supergenus *Bolitoglossa* (= "*Oedipus*" of the older workers), and *Batrachoseps* into the tribe Bolitoglossini, believing the latter to have originated from the Euryciini (his Hemidactyliini). Based on my studies and on reinterpretation of data previously published, however, the more reasonable interpretation is that the free tongue is diphyletic: the bolitoglossines being of *Plethodon* origin and distant from the eurycines.

If Wake's (1966) phylogenetic reconstruction of the tribes Hemidactyliini, Plethodontini, and Bolitoglossini is accepted, monophyletic origin of the free tongue is difficult to support. Deriving the latter two tribes independently from "hemidactyliines" presents only two possibilities: 1) the free tongue is monophyletic, indicating that the attached tongue in the Plethodontini is secondary, a most unlikely interpretation, or 2) the free tongue is diphyletic, the fixed tongue being primitive in the Plethodontini. The latter interpretation is the only reasonable one in Wake's context (as well as my own), especially considering the structure of the hyobranchial apparatus in *Plethodon* and its allies (see Lombard and Wake 1976, 1977). Except for common possession of the free tongue, bolitoglossines and euryciines share no characters indicating close relationship.

The *subvertebralis* of *Bolitoglossa* shows posterior flexures that are not intimately associated with the posterior basapophyseal regions of the vertebrae (contrast euryciines). *Hydromantes* has this flexure associated more closely with the transverse process. *Pseudoeurycea* has the posterior flexure extending beyond the posterior basapophyseal region. *Chiropterotriton* has species in which the *subvertebralis* is similar to that of *Bolitoglossa*, whereas other species lack all trace of posterior flexures, the subvertebral fibers being limited to passing between two adjacent vertebrae and ribs (compare Figs. 58, 59, and 60).

The trunk musculature of the supergenus *Bolitoglossa* and of *Hydromantes* is more readily derivable from the system of *Plethodon*, although admittedly evidence from a single character complex cannot provide definitive data against a connection with the Euryciini.

The cranium (see Wake 1966) is derivable from that of *Plethodon*, as is the throat musculature and hyobranchium (see Piatt 1935, Tanner 1952, Lombard and Wake 1976, 1977). Such a derivation is more parsimonious than Wake's (1966) proposal in that it does not call for hypothetical wanderings of taxa westward, but is consistent with known present distributions. Lombard and Wake (1977) have documented fundamental dissimilarity in the structures and mechanisms of protraction of the hyobranchium between the eastern and western free-tongued plethodontids, further corroborating the relationship between plethodontines and bolitoglossines.

The relationships of *Batrachoseps* are obscure, but I believe it to be most closely related to the Plethodontini (see Dunn 1926, Tanner 1952). Certainly no persuasive evidence against Dunn's original grouping has been proposed. If, as suggested by Wake (1966), *Batrachoseps* is closer to the supergenus *Bolitoglossa* than either of these is to *Hydromantes*, there are only two possibilities regarding the free tongue of the Bolitoglossini: 1) *Batrachoseps* has secondarily lost the free tongue, or 2) the free tongues of *Hydromantes* and of the supergenus *Bolitoglossa* are of separate origins.

The first possibility is unlikely and without any supporting evidence. The second possibility is also probably not true (although see Lombard and Wake 1977), making it necessary to reject close affinity of *Batrachoseps* and *Bolitoglossa*.

If the bolitoglossines are a monophyletic group, *Batrachoseps* must be more primitive than any of the former's living representatives. This means that it would be the plesiomorphic sister-group of

Hydromantes plus the supergenus *Bolitoglossa*. The evidence is not definitive (and *Batrachoseps* does share resemblances with the bolitoglossines, see Wake 1966), but I prefer to classify *Batrachoseps* within the Plethodontini. Although at least one species of *Batrachoseps* (*B. attenuatus*) has simplified subvertebral myomeres, as do at least some bolitoglossines (*Chiropterotriton chiroptera*), the distribution of this feature shows it to be all but certainly owing to convergence.

The Plethodontinae are, therefore, composed of two tribes, of which the Plethodontini are the most primitive and the Bolitoglossini are derived from it. The other plethodontid subfamily, the Desmognathinae, is probably derived from ancestry in common with the Plethodontinae and also composed of two tribes. With the removal of *Hemidactylium*, the Euryciini appear to be a natural group (see above descriptions, and data in Wake 1966, Lombard and Wake 1977). Within this group, both Dunn (1926) and Wake (1966) considered *Gyrinophilus* to be the most primitive. As regards cranial osteology, this seems true, but the structure of the trunk musculature creates complications. *Eurycea*, in some respects, perhaps presents a more primitive development of the axial musculature. That is, there is less accentuation of the posterior basapophyseal system and less emphasis of vertebral processes and crests (although these features may be secondary).

My theory of the relationships of the Plethodontini and Euryciini follows basically from the following morphocline in the structure of the trunk musculature:

Plethodon — *Hemidactylium* — *Eurycea* — *Gyrinophilus* — *Pseudotriton*.

This cline is not, however, claimed to be a phylogenetic sequence.

Hemidactylium is in many respects a structural ancestor for the Euryciini, as recognized by Wake (1966). A morphocline based on the cranium, for example, would be somewhat different, but probably the major obstacle to acceptance of the plethodontines as primitive with respect to the euryciines is the present belief that aquatic larvae are primitive to the Plethodontidae. There are indications that aquatic reproduction may be a secondary phenomenon, however.

Except for desmognathines, plethodontids possess only three branchial arches as embryos, larvae or both (see Piatt 1935, Dunn 1926). This could be taken as indicating reduction during an ancestral stage in which all plethodontids underwent direct development. Furthermore, the external gills of the larvae tend to be filamentous, as in the embryos of the genus *Plethodon*, rather than of the primitive form seen in hynobiids, ambystomatids, and even salamandrids (see Noble 1931, Bishop 1943).

The auditory apparatus of plethodontids seems to be basically an adaptation for terrestrial life (see Larsen 1963, Monath 1965, Reed 1920). The trunk musculature of *Plethodon* is unarguably more primitive than that of any member of the Euryciini or Desmognathini, while its cranial structure is at least equally primitive. The criterion of correlation of characters would indicate, although very tentatively, that perhaps the pattern of breeding is equally primitive.

Salthe (1967) shows that, where known, the courtship patterns of plethodontids are basically of a terrestrial sort. That is, the female is attracted to the dorsal region of the male's tail during spermatophore deposition, not to the cloaca as in ambystomatids and

salamandrids (which breed aquatically). In water, cloacal secretions generally provide the attractant. Salthe (1965) has argued for the terrestrial origin of plethodontids, based on the occurrence of lunglessness throughout the family.

The adaptation of the female brooding her clutch, whether on land or in water, is present throughout the family. All members of the Plethodontini have brooding, except for at least some species of *Batrachoseps* and this is probably a secondary adaptation to arid environments (Maiorana 1976, Dunn 1926, Bishop 1943). Bolitoglossines are probably all brooders, as are *Desmognathus*, *Leurognathus*, and almost certainly *Phaeognathus*, which is a terrestrial burrower (Dunn 1926, Martof 1962). Data on members of the Euryciini are less extensive. At least some *Gyrinophilus*, *Pseudotriton*, *Stereochilus*, and some *Eurycea* brood the young and it would seem probable that others have the same reproductive strategy (see Bishop 1943, Salthe and Mecham 1974). This kind of reproduction would probably most readily evolve in a terrestrial situation.

Desmognathus and *Leurognathus* have been extensively studied in terms of structure (Wake 1966, Dunn 1917, above descriptions) and life history (Dunn 1917, Organ 1961, Martof and Scott 1957, Martof 1962). Dunn (1917, 1926) and Organ (1961) noted the following relationships of the species of the two genera:

FOREST	<i>D. carolinensis</i> — <i>D. ochrophaeus</i>
BROOK	<i>D. monticola</i> — <i>D. fuscus</i> — <i>D. auriculatus</i> — <i>D. brimleyorum</i>
STREAM	<i>D. quadramaculatus</i>
AQUATIC	<i>Leurognathus marmoratus</i>

Moving both from bottom to top and left to right on the chart there is an increase in terrestriality, with a decrease in the length of the aquatic larval stage until it disappears. It has been assumed that those species having aquatic larvae are the most primitive in the group and that an evolutionary trend to increasing terrestriality is being reflected. However, it is perhaps not unreasonable to ask whether there might not be another interpretation. The *Desmognathus* group is highly derived, with numerous apomorphic character states in the cranium (Wake 1966) and trunk region (see above). Structurally there is no reason to assume the Desmognathini to be an early offshoot from plethodontid stock. Rather, they are most readily derivable from the structural plan exhibited by the Euryciini, being the culmination of the trends exhibited by the latter. Only the breeding pattern would indicate early derivation.

The reproductive pattern of *Desmognathus fuscus* is well understood and sheds light on the question of the primitive nature of aquatic reproduction. "The eggs are guarded by the mother [on land] The period from laying to hatching is about five weeks. When hatched the larvae measure 15 mm. There is a terrestrial larval stage of 15 to 16 days. At the expiration of this period the length is about 20 mm. and the larvae enter the water" (Dunn 1917, p. 411). This increase in size during the terrestrial phase may indicate that food is taken. Noble (1931, p. 56) noted that "the young Dusky Salamander [*D. fuscus*], during the first two weeks of its life, is not merely a larva which chances to be hatched at a distance from its aquatic habitat, but it is a terrestrial salamander fully able to move

about in the damp cracks and crannies leading from the nest to the nearest pool." The tail fin and gills, which lack distinct central rami and are somewhat filamentous, develop only upon the larva's entering the water.

Wilder (1917, p. 17) stated: "That the terrestrial larval stage [of *D. fuscus*] is really a definite one is shown by the behavior of the newly hatched larvae when placed in water . . . they will not remain in the water, but persistently crawl out It is not until all external evidence of the yolk mass has disappeared that they will remain in the water." Noble and Evans (1932, p. 8) "found that *Desmognathus fuscus fuscus* was able to pass through its larval stage on land without having access to free water," but that it was also possible to force them to become aquatic immediately upon hatching. This indicates plasticity in development. These facts intimate that the aquatic "larval" phase has perhaps been secondarily added to the life-cycle and that those members of the Desmognathini that lay aquatic eggs may do so secondarily.

Rather than interpreting the sequence as stream to stream-bank to forest as diagrammed above, it is equally possible that the desmognathine sequence is forest to stream-bank, or stream-bank to both forest and stream. If either of the latter is true, then justification for continued recognition of the genus *Leurognathus* is slight. Under this new view, *Leurognathus* fits well into the morphocline of the genus *Desmognathus*.

In spite of the various facts tending to support the theory, there are certain problems with its acceptance. These include:

retention of a coronoid in larvae of some plethodontids, the four branchial arches of larval desmognathines (as opposed to three in other plethodontids), and the coherent theory of the mountain-brook origin of the lungless condition. These urge caution in the evaluation of the hypothesis here proposed, and there are several alternative possibilities:

1. The aquatic larvae of the Euryciini and Desmognathini are primitive, as suggested by previous workers. This would indicate a sister-group relationship between the Plethodontinae (terrestrial eggs) and the Desmognathinae (aquatic larvae), with each unit retaining certain primitive features and having developed other, apomorphic ones.

2. The aquatic larva of all plethodontids is secondarily derived, the reproductive pattern of the Plethodontini and Bolitoglossini being primitive.

3. Various combinations of alternative two: perhaps the Euryciini are secondarily aquatic and the Desmognathini primarily so, or vice versa.

At present, although I would urge careful consideration of the second possibility, the first alternative is probably the most reasonable.

The Plethodontidae are, therefore, to be divided into two sub-families sharing a sister-group relationship. The Plethodontinae consist of two tribes, the Plethodontini and the Bolitoglossini, which are united on the basis of reproductive patterns, axial musculature, and basic osteology. The Desmognathinae are also comprised of two tribes, the Euryciini and the Desmognathini, which share a common sort

of reproduction, the same basic plan of trunk musculature, similar osteology, and inhabit a common geographical area. What I believe to be the phylogenetic relationships of these higher taxa is shown in Figure 100, and the classification is given in Table 2. It is not profitable to attempt a lower-order phylogenetic reconstruction of the Plethodontidae. Any sort of generic phylogeny can be little more than more or less untestable guesses in this family.

Although, at first sight, it may appear that my phylogenetic reconstruction (Fig. 100) and classification (Table 2) disagree to a major extent with those of Wake (1966), such is not the case. Wake (1966) recognized the primitive nature of *Hemidactylium* within his tribe Hemidactyliini. I agree that it is probably related to *Eurycea*, but also that it is related to the *Plethodon* group. As its trunk musculature, lack of a free tongue, and secondary return to aquatic reproduction (Dunn 1926) all differ from members of the Euryciini, and as it shares features that are derived with respect to the Plethodontini, but primitive with respect to the Euryciini, it fits better with the former tribe. Wake (1966) also recognized the relationship of the Desmognathini to the Euryciini. My scheme simply indicates a closer relationship, as anticipated by Noble (1927). The major difference in our interpretations concerns the bolitoglossines, which I, in agreement with Piatt (1935), consider derived from the Plethodontini. This fits better with present geographic ranges, anatomical evidence (hyobranchial, osteological, and axial), and breeding data than the theory of Wake (1966).

The Plethodontidae are closely related to both the Ambystomatidae and to the Salamandridae. As argued below, I consider the family to be best grouped with the families having posterior basapophyseal musculature, as this reflects a basic adaptive shift and allows splitting of the Caudata into two subequal suborders.

viii) Proteidae Hogg 1838

CONTENT. *Proteus* Laurenti 1768, *Necturus* Rafinesque 1819, ?*Orthophya* von Meyer 1845, ?*Hylaeobatrachus* Dollo 1884.

FOSSIL RECORD. The fossil record of proteids is spotty and of uncertain interpretation. *Comonecturoides marshi*, represented by a single right femur from the Upper Jurassic of Wyoming, was referred to the "Necturidae" by Hecht and Estes (1960), but the proper classification of this monotypic genus is uncertain. Herre (1935b) described *Palaeoproteus* from the Eocene of Europe as a primitive proteid, but Estes et al. (1967) referred it questionably to the Salamandridae. Arguments for classifying it with the Batrachosauroididae are presented below.

Hylaeobatrachus croyi Dollo 1884 from the Lower Cretaceous of Belgium is also of uncertain relationship. Although Wiedersheim (in Dollo 1884) considered it to be a salamandrid, it is usually referred to the Proteidae (see Kuhn 1962). If truly a Proteid, it is very primitive: there are only 17 presacral vertebrae, there are four toes on the front and five on the hindlimbs, and well-developed maxillae are present (see Kuhn 1962, Dollo 1884, figs. 1 and 2). On the other hand, it is definitely paedogenic, with external gills and

three ossified branchial arches. Although the type specimen has been lost, Estes is presently studying the counterpart.

Vertebrae of *Necturus* from the upper Paleocene Ravenscrag Formation of Saskatchewan have recently been discovered (see Fig. 13) and are described elsewhere (Naylor 1978b). *Necturus* is questionably known from the Oligocene of North America (Romer 1966, Estes pers. comm.). Lynch (1965) reported vertebrae of *Necturus* from Florida, which are somewhat outside the present range of the genus.

Two species of *Orthophya* have been named from the Miocene of Switzerland (von Meyer 1845). This genus is usually referred to the Proteidae (Brame 1967, Kuhn 1962), but all known material has been lost. Estes and Darevsky (1977) name a new genus and species of Proteid, *Mioproteus caucasicus*, from the Miocene of the Caucasus, which they suggest might be the same as *Orthophya*. *Mioproteus* has relatively robust vertebrae with distinct posterior basapophyses and a ring of calcified tissue within the anterior cotyle. It shows resemblances to batrachosauroidids, as well as to *Necturus* and (especially) *Proteus*. *Proteus bavaricus* is based on a parasphenoid from fissure fillings of Pleistocene age in Germany (Brunner 1956), but as noted by Estes and Darevsky (1977) the figure and description of this material are inadequate.

The known fossils contribute little to understanding of the relationships of the Proteidae, but further study of known specimens might well produce valuable information.

RELATIONSHIPS. Before discussing the relationships of proteids to other salamanders, it is necessary to consider the kinship of *Necturus*

and *Proteus*. Following an earlier argument of Hecht's (1957), Hecht and Edwards (1976) attempted to demonstrate that *Proteus* and *Necturus* are not especially related. Although characters are rejected as having no phylogenetic information owing to their being loss characters, presumably primitive, or paedogenic, no positive data are presented in support of the thesis. Positive evidence for monophyly has been presented in various papers. Kezer and his co-workers have provided strong karyological evidence of the close relationship of proteids (Kezer, Seto, and Pomerat 1965, Leon and Kezer 1974). Larsen and Guthrie (1974) present data from the skull, auditory region, and hyobranchium that are in support of a theory of monophyly. Study of the trunk musculature (see above) and of spinal nerve exits (Edwards 1976) indicate relationship. Indeed, taken together, the characters listed by Hecht and Edwards (1976) demonstrate the probability of monophyly.

There is often a tendency to use paedogenesis or neoteny to exclude characters from consideration and to "explain" the existence of features. Paedogenesis and neoteny are not equivalent phenomena as regards their expressions in the different families of salamanders. Although owing to the retention of larval features in breeding adults, the expression of paedomorphosis is highly variable. Hynobiids, ambystomatids, plethodontids, and salamandrids all have neotenic (facultatively metamorphosing) representatives, but none could be confused with those of another family. Cryptobranchids, amphiumids, proteids, sirenids, and some plethodontids are, to a greater or lesser degree, paedogenic. Nonetheless, each family is distinct structurally

and ecologically, and if fossil forms are considered, the Scapherpetontidae and Batrachosauroididae are also distinctive paedogenes. The important point is that, within the adaptational strategy termed paedogenesis, there is a wide variety of distinctive structural plans and *Necturus* and *Proteus* share one of these. Owing to differences in ancestry and consequent selection, distinctive structural changes have taken place in each family. This is especially important in view of the fact that *Necturus* and *Proteus* have quite different ecological relationships, indicating that the similarities are owing to descent.

It is invalid, therefore, to dismiss characters uniquely shared between *Proteus* and *Necturus* as paedogenic or primitive, thereby implying that they mean nothing. Whereas one or two such characters could be so treated, fourteen such characters cannot be rejected. In total, the character states shared by proteids serve to clearly distinguish them from all other paedogenic and neotenic urodeles and, at the same time, provide overwhelming evidence for monophyly.

The features considered by Hecht and Edwards (1976) include:

1. *The perennibranchiate condition.* This differs from apiumids and cryptobranchids, and the gills differ structurally from those of other perennibranchiates.
2. *Presence of two gill slits.* Although paedogenic, this feature is unique amongst "larval" salamanders.
3. *Proportions of the skull.* Again, although in a limited sense "paedogenic," these proportions are unique to the Proteidae.
4. *Absence of maxillae, septomaxillae, lacrimals, nasals, and prefrontals.* These features are treated as having no taxonomic

information owing to their being "loss characters." Nevertheless, although perhaps of minor importance, such losses do provide some phylogenetic information, especially when taken together and in combination with other data. The loss of all these bones is unique to the Proteidae, indicating monophyly.

5. *Broad parasphenoid*. Certainly a "larval" condition, but, as noted by Estes (1975, p. 372), its "close approximation to the condyles is unusual," and the overall shape is also unique.

6. *Separate opisthotic*. This unique character was rejected as having no information content owing to its presumed paedogenic nature. Hecht and Edwards (1976) note that certain larval salamanders show three separate regions of ossification in the otic region. Cloete (1961), although cited by these workers, makes no mention of a separate opisthotic centre of ossification in *Rhyacotriton* that I can find. Bonebrake and Brandon (1971, pp. 199-200) state that "the ossifying opisthotic expands over the posterior surface of the otic capsule in stage VI [and] it reaches and fuses indistinguishably with the dorsal process of the exoccipital" in *Ambystoma texanum*. Parker (1878, cited in Bonebrake and Brandon 1971) described a separate opisthotic in *Ambystoma mexicanum* (as *Siredon*) and *Siren*.

Although it is, therefore, true that the presence of the opisthotic *per se* may not represent a shared-derived character in proteids, this does not settle the question. The opisthotic is retained in both *Necturus* and *Proteus* as a separate element in the adult, not merely as a transitory stage. It is expanded in the same way and distinctly altered to the same shape in both genera. This common character is

thus almost certainly a shared-derived character, indicative of close genealogical relationship.

7. *Non-pedicellate teeth*. This feature is larval, but the development is similar in each genus, with a zone of weakness (see Means 1972, Larsen and Guthrie 1974).

8. *Hyobranchium*. The similarities are dismissed as "larval" and "primitive." First of all, the hyobranchium is all but certainly not primitive, but highly apomorphic (compare that of hynobiids, Edgeworth 1923). Secondly, although the resemblances are, to a certain extent, owing to paedogenesis, they are also derived. That is, the hyobranchium of each genus is more similar to that of the other than to that of any other "larval" salamander (see Larsen and Guthrie 1974, Cope 1889).

9. *Chromosome data*. These are dismissed as not "certain evidence of monophyly" (Hecht and Edwards 1976, p. 666), but the common possession of a chromosome number of $n=19$, and close similarities in the structures of individual chromosomes between the genera do provide positive and important support (not, of course, proof or "certain evidence") for an hypothesis of monophyly (see data in Kezer et al. 1965, Morescalchi 1975). It is possible that the number of $n=19$ and the similar structures developed convergently, but this is certainly less likely (especially in light of the other anatomical evidences) and unparsimonious. References to ultimately non-explanatory concepts of "karyotypic orthoselection" are not sufficient to explain away these similarities.

10. *Pattern of spinal nerve exits*. This shared character state is dismissed as "primitive" and, therefore, not to be "considered

evidence for monophyly or phyletic affinity" (Hecht and Edwards 1976, p. 664). However, shared characters, even though judged primitive by a researcher, do hold information as to the relationships of taxa. The spinal nerve data are also of interest in light of the structure of the axial musculature of proteids. Both genera have closely similar patterns in the *dorsalis trunci*, *subvertebralis*, and lateral abdominal musculature. These patterns are consistent only with derivation of *Proteus* and *Necturus* from an ancestor having opisthocoelous or proto-opisthocoelous vertebrae (that is, from a relatively derived ancestor). It is, therefore, likely that the complete lack of intra-vertebral postatlantal exits for spinal nerves is a secondary phenomenon (only cryptobranchoids and batrachosauroidids have this pattern amongst other salamanders). If this interpretation is true, then the common lack of spinal nerve exits except through the atlas is a shared and derived character.

11. *Loss of the fourth branchial arch.* Owing to its nature (a loss character), this feature cannot be given major taxonomic weight, but in combination with the other features it is another positive evidence.

12. *Distribution of the palatal teeth.* This is rejected as a "larval" condition, which is (in a very limited sense, compare hynobiids and ambystomatids) true. Nevertheless, and more to the point, this condition clearly distinguishes both *Proteus* and *Necturus* from other paedogenic salamanders. The distribution of the palatal teeth is to be regarded as a shared and derived character, which has evolved via pedomorphosis.

13. *Absence of ypsiloid cartilage.* This feature is claimed to be of low taxonomic importance in that it is a loss character. This is true to the extent that the ypsiloid has been lost convergently in several other groups (e.g., amphiumids and plethodontids), but the common presence of the anterior cartilaginous projection from the pubis in *Necturus* and *Proteus* is an apomorphic character.

It is not sufficient to state that "the form of the sacral projections was different in the two genera, implying that they developed independently" (Hecht and Edwards 1976, p. 664), nor does Hecht's (1957) claim that it is a "neotenic adaptation" explain away the structure. Other paedogenic or neotenic urodeles lack all trace of an anterior projection from the pubis. *Cryptobranchus*, which is elongated to much the same extent as *Necturus* and also paedogenic, lacks the projection and retains the ypsiloid. In *Amphiuma* the ypsiloid is lacking, but no projection develops. In larvae and neotenes of other families a fully functional ypsiloid is usually present. If absent, as in plethodontids, no special projection develops.

The absence of the ypsiloid and its replacement by the triangular cartilage extending from the pubis is an apomorphic feature shared by the two genera and is another significant positive evidence for monophyly.

14. *Structure of the columella.* This feature is rejected by Hecht and Edwards as being of minimal importance owing to "heterotropic" origin and dependence on allometry. Once again the detailed similarity between *Proteus* and *Necturus* is overlooked and the common

lack of an operculum dismissed. Larsen and Guthrie (1974) have demonstrated detailed resemblance in the structure of this region between the two proteids. More or less vague resemblances to *Ambystoma mexicanum* cannot be validly used to cause rejection of this shared and derived character. Furthermore, the common development of a structure, whether owing to allometry or anything else, provides evidence potentially in support of genealogical relationship. Allometry and neoteny may well affect the development of certain structures, but such statements ultimately say little as to their apomorphic status.

If further evidence were required, data from my studies of the trunk musculature show close and detailed resemblance of the epaxial and hypaxial units. These resemblances are almost certainly characters derived from a common ancestor, and differ from those of all other paedogenic salamanders. Rejection of the similarities of the trunk musculature as paedogenic, primitive, allometric, or owing to orthoselection is not plausible.

It is to be concluded that the characters presented by Hecht and Edwards (1976) provide very good evidence for a theory of monophyly for *Proteus* and *Necturus*. Even if true that an argument can be made that any given character should, by itself, not be accorded major taxonomic weight, when the characters are considered together they are important and convincing. In systematics one treats entire organisms, not isolated characters. It is necessary to be concerned with what the characters altogether mean, not with mere descriptive discussion of them (i.e., that a feature is neotenic, paedogenic, owing to loss,

primitive, or whatever). Characters judged to be in any of these categories often still carry important taxonomic and phylogenetic information. Proteids are, therefore, to be considered as most probably a monophyletic group, the polyphyletic hypothesis having been shown to be very unlikely (see also Kezer et al. 1965, Brandon 1969, Leon and Kezer 1974, Larsen and Guthrie 1974).

Knowledge of the relationships of the Proteidae to other salamanders has been uncertain. Cope (1889) suggested that proteids were very primitive and placed them in a separate order in a position ancestral to his order Urodela. Reed (1920), on the basis of the auditory apparatus, included them in a legion along with plethodontids and amphiumids. Dunn (1926) classified proteids in his Salamandroidea, along with the "higher" salamanders (ambystomatids, plethodontids, amphiumids, and salamandrids), but noted that they were "not obviously related to any one of the other families" (p. 3).

Noble (1931, p. 483), however, placed them in a separate suborder, stating that they "form a natural group . . . of unknown ancestry," but perhaps derived from salamandrids. He noted that the cloacal glands resemble those of amphiumids, salamandrids, and plethodontids. Herre (1935b), basing his conclusions on osteology and the Eocene *Palaeoproteus*, derived proteids from the salamandrid newts. Wake (1966) divided proteids into separate families (Necturidae and Proteidae), which he placed with salamandrids and amphiumids in the suborder Salamandroidea. Regal (1966) utilized only the single family Proteidae, placed alone in the Proteida.

Salthe (1967) suggested that what is known of the breeding of *Proteus* resembles that of *Triturus* and that courtship could be taken to indicate that proteids were diphyletic. As the courtship of *Necturus* is all but unknown, however, these data are not convincing. Primarily on the basis of karyology, Morescalchi (1973, 1975) derived proteids from ancestry close to that of the Sirenidae and in common with that of the "higher" salamanders (those families having internal fertilization). Leon and Kezer (1974), also on the basis of chromosomal data, suggested that proteids and salamandrids share a common ancestor. Most recently, Edwards (1976) produced a cladogram that shows proteids as the plesiomorphic sister-group of batrachosauroidids, amphiumids, plethodontids, ambystomatids, scapherpetontids, and salamandrids.

In spite of uncertainty regarding the affinities of the Proteidae, it is now possible to develop a well-based hypothesis of relationships. Estes (1975) suggested that the Batrachosauroididae are closely related to proteids. It will be argued that this hypothesis is the most reasonable in light of the fossil evidence, comparative osteology, and information from the trunk musculature. Estes noted resemblances between *Opisthotriton* and proteids in the structure of the squamosal (with a columellar process), the vomers and vomerine teeth, the broad posteriorly produced parasphenoid, structure of the teeth (non-pedicellate), "general aspect" of the hyobranchial skeleton, and the *Necturus*-like vertebrae of *Opisthotriton*. In addition to these, the following are also general resemblances between the two families: the structure and relationships of the vomers and palatines and of the associated teeth, the premaxillae with long and separate nasal

spines, the small odontoid process of the atlas, and the caudal vertebrae with long, tubular hyperapophyses and haemal spines. These general and specific resemblances are very suggestive.

The relationship is further indicated by considerations of the trunk musculature in Recent proteids, the theory of the development of opisthocoely presented above, the new Miocene proteid discovered in the Caucasus (Estes and Darevsky 1977), and the spinal nerve data presented by Edwards (1976). Batrachosauroidids, having opisthocoelous vertebrae, could only have evolved from ancestors having posterior basapophyseal musculature (see above, also Figs. 94, 95, 96, and 97). *Opisthotriton* and *Prodesmodon* (as reinterpreted, Naylor 1978a) have well-developed posterior basapophyses, confirming the presence of such musculature. Opisthocoely also correlates, at least among living salamanders, with a general simplification of the *dorsalis trunci*.

With respect to proteids, which are fully amphicoelous, the structure of the trunk musculature indicates derivation from an opisthocoelous ancestor (compare descriptions of proteids, plethodontids, and cryptobranchids above). The *dorsalis trunci*, although massive, has a simplified myoseptal pattern, while the *subvertebralis* is very simple in comparison to that of cryptobranchoids and ambystomatoids, retaining only posterior flexures. Derivation of the proteid pattern of trunk musculature directly from the anterior basapophyseal sort without an intervening stage such as that represented by the Batrachosauroididae is unlikely. The newly discovered *Mioproteus* further supports this suggestion. The vertebrae possess posterior basapophyses and a ring of calcified tissue inside the anterior cotyle,

the latter perhaps being a remnant of opisthocoely. *Mioproteus* thus shows resemblance to both batrachosauroidids and proteids (see Estes and Darevsky 1977 for figures and descriptions).

Proteids are also like batrachosauroidids in the pattern of the spinal nerve exits (see Edwards 1976) and the overall structure of the atlantes, with small or nonexistent odontoid processes. Further evidence of the suggested relationship can, perhaps, be gained from the following morphocline of vertebral structure (this does not purport to be a phylogenetic event, but probably is consistent with such a sequence):

	<i>Batrachosauroides</i>	<i>Necturus</i>
<i>Prodesmodon</i> — <i>Opisthotriton</i> —		—
	<i>Palaeoproteus</i>	<i>Proteus</i>

In this series (see Fig. 12, also Estes 1964, figs. 38, 41 and 42, 1969a, figs. 1, 3 and 5) is documented progressive reduction of the degree of opisthocoely and of basapophyses down to complete loss. This could well be the actual structural sequence involved in the evolution of proteids, but no ancestor-descendant relationships are claimed.

If close relationship between proteids and batrachosauroidids is accepted, they must be clasified together. I prefer to follow Estes (1975), who recognized two families in a single higher taxon, here the superfamily Proteoidea. The problem is now a resolution of the position of this superfamily within the Caudata.

Proteoids possess several characters forbidding close affinity with the Cryptobranchoidea: elongate premaxillary spines, fusion of angular and prearticular in the lower jar, and (at least in proteids)

internal fertilization by means of a spermatophore. Distinction from the Ambystomatoidea is shown by the possession of opisthocoelous vertebrae or simplified, posterior basapophyseal musculature. On the basis of these features, the Proteoidea may be separated from the more primitive urodeles (the Cryptobranchoidea and Ambystomatoidea, see above) and united with plethodontids (the Plethodontidae) and salamandrids and sirenids (the Salamandroidea, see below). Affinity to the latter superfamilies is also indicated by the reproductive patterns of *Necturus* and *Proteus*. In *Necturus* eggs are laid singly, attached to the undersurfaces of large rocks, as in plethodontids and salamandrids, but unlike ambystomatids, whereas *Proteus* gives birth to live young, as in *Salamandra* (see Boyden and Noble 1933).

The precise relationships of proteoids to the other more derived salamanders is uncertain. If truly primitive, the higher chromosome number (see Morescalchi 1975) and lack of intervertebral postatlantal spinal nerves (see Edwards 1976) would forbid close relationship with plethodontids and salamandroids and indicate relatively early derivation from a more basal stock. In light of the advanced nature of the axial musculature and cranial osteology, however, these two characters may be secondary. The karyotype is probably a plastic, adaptive part of the phenotype, likely to change readily in response to selective pressures (see above). Although Edwards (1976, p. 313) claimed that "the spinal nerve patterns are acquired very early in ontogeny and are not affected by metamorphosis," this is only partially true. Young larvae of at least some salamandrids have spinal nerves that exit intervertebrally. This is true for small *Pleurodeles* larvae (see

Mauger 1962), as well as for the very young larvae of *Triturus vulgaris* and larvae within the oviducts of *Salamandra* (personal observation).

This shows the strong possibility that the spinal nerve patterns of proteoids are a secondary, paedomorphic phenomenon.

At present it is not possible to be very specific as to times of origin. I prefer, tentatively, to derive proteoids from the primitive stock that eventually gave rise to the plethodontoids and salamandroids, but prior to the divergence of the two latter groups (see Fig. 104).

ix) Batrachosauroididae Auffenberg 1958

CONTENT. *Batrachosauroides* Taylor and Hesse 1943, *Opisthotriton* Auffenberg 1961, *Prodesmodon* Estes 1964, *Palaeoproteus* Herre 1935, *Piceoerpeton* Meszoely 1967.

RELATIONSHIPS AND OCCURRENCES. *Batrachosauroides dissimulans*, based on a single complete skull, now lost, from the middle Miocene of Texas, was named and described by Taylor and Hesse (1943). These authors referred the genus questionably to the Salamandroidea of Noble (1931), as closest to the amphiumids. Auffenberg (1958) later referred vertebrae and atlantes from Texas to the species and also erected a new monotypic family, the Batrachosauroididae, which he placed in the Salamandroidea. Estes (1963) reported an atlas of *B. dissimulans* from the lower Miocene of Florida. A new species, *B. gotoi*, from the lower Eocene of North Dakota was named by Estes (1969a). It was based on a trunk vertebra, with dentaries of aspect similar to those of *B. dissimulans* being referred.

Auffenberg (1961) named and described a new genus and species from the Lance Formation of Wyoming, *Opisthotriton kayi*, and also referred lower Paleocene material from Montana to the species. *O. kayi* was based on a trunk vertebra, with atlantes and cranial material being referred. Estes (1964) showed subsequently that the figured maxilla belonged to *Scapherpeton tectum*, however. Auffenberg (1961, p. 464) assigned *O. kayi* to the Salamandridae on the basis of the opisthocoelous centra, but stated that it might "eventually be assigned to the *Plethodontidae* [sic], or to an extinct family."

Working with more extensive material from the Lance Formation, Estes (1964) provided figures and detailed descriptions of *Opisthotriton*. Numerous vertebrae, atlantes, vomers, dentaries, maxillae, and premaxillae were referred to the species *O. kayi*. Estes noted resemblances to desmognathines (with which he provisionally classified the genus) and also to *Necturus*. *Opisthotriton* is known from other Upper Cretaceous horizons: Hell Creek Formation, Kirtland and Fruitland formations, Upper Milk River Formation (= Eagle Formation), Oldman Formation (= Judith River Formation), and Judith River Formation (Estes et al. 1969, Sahni 1972, Fox 1972, 1976).

Estes (1969a) classified *Opisthotriton* with *Batrachosauroides* in the Batrachosauroididae, which was claimed to be related to the Scapherpetontidae. Both of these families were placed in the Ambystomatoidea, along with ambystomatids and plethodontids. At the same time, a skull of *Opisthotriton* from the upper Paleocene Polecat Bench Formation was figured and described. Estes (1975) later argued that batrachosauroidids were related to proteids, a conclusion that my findings strongly support (see above).

Prodesmodon copei was named and described from material from the Upper Cretaceous Lance Formation, the type specimen being a trunk vertebra (Estes 1964). Atlantes, premaxillae, maxillae, and dentaries were referred to the species, which was tentatively classified in the Plethodontidae. Subsequently, Estes (1969c) classified *Prodesmodon* with the Lower Cretaceous *Prosiren* in the Prosirenidae. This was done on the basis of the supposed common possession of unique jaw material. I have shown elsewhere (Naylor 1978a) that jaw elements have been incorrectly ascribed to *Prodesmodon* and that the dentaries named *Cuttysarkus* are properly referred to *Prodesmodon*, as is a newly discovered vomer (UA 12095). These elements are very similar to those of *Opisthotriton*, as are the vertebrae, and *Prodesmodon*, as reinterpreted, is a member of the Batrachosauroididae (see Naylor 1976, 1978a), and includes *Cuttysarkus* as a junior synonym.

Herre (1935b) named and extensively described *Palaeoproteus klatti* from the middle Eocene Geiseltales browncoal. This species is known from a series of partial and complete skeletons and was referred by Herre to the Proteidae. It is elongate with small limbs and the skull is long and narrow, with the bones being relatively robust and solidly sutured. Prefrontals and nasals are lacking and there are very long premaxillary spines (compare *Opisthotriton* in Estes 1969a, fig. 4). Herre's figure (1935b, Abb. 6) shows that the parasphenoid is broad and posteriorly produced, as in proteids and batrachosauroidids (see also Estes 1975). Only a single element is found in the *fenestra ovalis*. This was called an "operculum" by Herre, but it is undoubtedly

a columella, as elsewhere he refers to the columella of *Proteus* as an operculum.

Estes et al. (1967) later named and described a new species of *Palaeoproteus*, *P. gallicus* from the Paleocene of France. At the same time, they questionably referred the genus to the Salamandridae on the basis of the suggested approach to opisthocoely, forked ribs, wide separation of the head and trochanter in the femur, and the "general shape" and robustness of the cranial bones. The figured atlas of *Palaeoproteus* is all but identical to those of *Opisthotriton* and *Prodesmodon*, while the dentary is very similar in the three genera (Estes et al. 1967, figs. 1 and 3). Estes et al. (1967) noted the resemblances of *Palaeoproteus* to *Opisthotriton*, and Estes (1969a) recognized the same close similarity and probable relationship, but did not formally place *Palaeoproteus* within the Batrachosauroididae. Based on the data presented by Herre (1935b) and Estes et al. (1967), the conclusion that *Palaeoproteus* is to be classified with the batrachosauroidids is all but inescapable. Larsen and Guthrie (1974) suggested that *Palaeoproteus* is related to the Proteidae. There are certainly similarities, but even more are evident in comparison of the genus with batrachosauroidids. The resemblances of *Palaeoproteus* to proteids are, however, further evidence of the relationship between these two families.

Abundant material of *Piceoerpeton* from the Paleocene Ravenscrag Formation of Saskatchewan indicates that this genus is probably a member of the Batrachosauroididae (Naylor and Krause, in prep.). As argued by Estes (1975) and discussed above, the Batrachosauroididae are to be united with the Proteidae in the superfamily Proteoidea.

x) Salamandridae Gray 1825

CONTENT. *Salamandra* Laurenti 1768, *Chioglossa* Bocage 1864, *Pleurodeles* Michahelles 1830, *Tylototriton* Anderson 1871, *Salamandrina* Fitzinger 1826, *Notophthalmus* Rafinesque 1820, *Taricha* Gray 1845, *Cynops* Tschudi 1838, *Paramesotriton* Chang 1935, *Hypselotriton* Wolterstorff 1934, *Pachytriton* Boulenger 1878, *Triturus* Rafinesque 1815, *Neurergus* Cope 1862, *Euproctus* Gené 1838. In addition to these extant genera, the following fossil genera have been named: *Palaeosalamandra* Herre 1949, *Praesalamandra* Brunner 1957, *Megalotriton* Zittel 1888, *Voigtiella* Herre 1949, *Palaeosalamandrina* Herre 1949, *Palaeopleurodeles* Herre 1941, *Dehmiella* Herre and Lunau 1950, *Polysemia* goldfuss 1831, *Heliarchon* von Meyer 1964, *Grippiella* Herre 1949, *Tischleriella* Herre 1949, *Chelotriton* Pomel 1853, *Oligosemia* Navas 1922, *Archaeotriton* von Meyer 1859, *Brachycormus* Herre 1949, *Heteroclitotriton* De Stefano 1903, *Koalliella* Herre 1950.

FOSSIL RECORD. Except for a French Miocene record of *Chioglossa* reported by Estes and Hoffstetter (1976), the fossil occurrences of salamandrids and the possible relationships of the taxa have been discussed under the anatomical descriptions of the individual species above.

RELATIONSHIPS. Intergeneric relationships within the Salamandridae have been uncertain. Bolkay (1928), basing his conclusions on cranial osteology, believed *Euproctus* to be primitive, not only to salamandrids, but with respect to ambystomatids as well. This scheme is in conflict with other anatomical evidence and with logical inference of phylogeny.

Nevertheless, Bolkay (1928) did conclude that *Salamandra* and *Chioglossa* were primitive with respect to the other newts. Herre (1935b) also believed that these two genera were the most primitive members of their family.

Noble (1931) considered the following features to be primitive for salamandrids:

1. Bony frontosquamosal arch.
2. High neural crests.
3. Long ribs.
4. Four-pronged basihyal in hyobranchium.
5. Single, simple *rectus abdominis*.
6. Presence of an *obliquus internus*.

These features are exhibited by one or another of the newts, notably *Tylototriton*. With the exception of the fourth feature, it is all but certain that all are derived. On the basis of ex-group comparisons, these features are shown to be apomorphic for the Salamandridae. As *Salamandra* and *Chioglossa* lack these character states, which are also lacking in more primitive families (hynobiids, ambystomatids, and plethodontids), it is not reasonable to assume secondary loss to account for the conditions in these two genera (see below).

In the most recent study of the intrafamilial relationships of salamandrids, Wake and Özeti (1969) developed a detailed generic phylogeny. Although probably in large part correct, certain of their results reflect misinterpretations and an over-reliance on a single adaptational system, the hyobranchium. I suggest that their 40 characters fall into the following categories (numbering follows Wake and Özeti 1969):

A. Those probably correctly identified as primitive or derived and, therefore, of value in phylogenetic reconstruction:

1. Separate premaxillae.
13. Presence or absence of the second basibranchial (bb2).
14. Presence or absence of the epibranchial.
15. One or two pairs of radii on first basibranchial.
16. Presence or absence of an interrachial cartilage. This is, however, linked to the number of pairs of radii and, therefore, not deserving of status as a separate character.

B. Those correctly identified as primitive or derived, but carrying little or no phylogenetic information:

7. Loss of the fifth toe. This is found only in *Salamandrina* and is thus an autapomorphy as well as a loss character (see Hennig 1966, Hecht and Edwards 1976).

8. Reduction of the lungs. This is convergent in species inhabiting mountain streams (see Wilder and Dunn 1920).

12. Reproductive pattern. Only *Salamandra* gives birth to live young; the other genera lay eggs. This feature is, therefore, an autapomorphy.

C. Those of equivocal status and, therefore, of low phylogenetic value:

5. Ossification of the operculum.
6. Presence of caudosacral ribs (this may be truly primitive, however).
10. Size of eggs.
17. Ossification of the first basibranchial.
18. Ossification of the first ceratobranchials.

D. Those incorrectly, or not identified as to primitive or derived state:

2. Frontosquamosal arch. This structure is also lacking from all other families, as well as from *Salamandra* and *Chioglossa*. It is, therefore, not reasonable, parsimonious, or logical to consider the structure primitive with respect to the Salamandridae. The fronto-squamosal arch gives the newt skull a superficially archaic (or "primitive") aspect, but bears little resemblance to the structures of truly primitive amphibians (see Romer 1966, Bolt 1969).

3. Length of maxillae. As short maxillae are found in all of the more primitive families of salamanders, as well as in certain salamandrids, it is not reasonable to assume a long maxilla to be primitive to the family.

4. Medial contact of nasals. The nasals overlap the elongate premaxillary spines in some newts, but this is a highly derived condition secondarily convergent upon that of hynobiids (compare ambystomatids, plethodontids, and salamandrines).

9. Texture of the skin. As rough skin was correlated with features incorrectly judged to be primitive (e.g., the frontosquamosal arch, nasals in medial contact, and elongate maxillae), it too was considered primitive. As the correlated features are more reasonably derived and because rough skin is lacking in all of the more primitive families, there is no evidence for assuming rough skin to be primitive for the Salamandridae.

11. Courtship pattern. The pattern of *Euproctus* was assumed to be primitive on the basis of Salthe's (1967) work. However, courtship

patterns within the Salamandridae compared with those of other families makes this conclusion unlikely. Courtship in *Euproctus* differs markedly from that of other newts, with the male capturing the female by means of his tail. It is probable that the pattern of *Euproctus* is highly derived, adapted to the mountain streams and rivers in which it lives, and it is not reasonable or parsimonious to hypothesize plesiomorphy. The courtship of *Euproctus* could well be derived from that of *Triturus*, which also uses the tail as an important component in courtship, although in a different fashion (Salthe 1967). The courtship of *Salamandra* and *Chioglossa* (Salamandrinae) and of *Tylostotriton*, *Pleurodeles*, and *Salamandrina* (Pleurodelini) is the same (capture from beneath with the anterior limbs, see Salthe 1967) and correlated with structural primitiveness. It is probably the most primitive for the family (see also Salthe and Mecham 1974).

40. Contact of the maxilla and pterygoid. This feature is unique to a few Asian newts, found in no other families of salamanders (except one ambystomatid), and basically different from maxillary-pterygoid contact in other amphibians. It is, therefore, a derived character state.

E. Those characters coming from a single functional system (the hyobranchial apparatus) and, therefore, probably not deserving of minute subdivision. These include the remainder of the characters.

Clusters developed from computer analysis do not necessarily reflect phylogenetic events, especially if the majority of the features come from a single integrated system. Before clustering can have phylogenetic meaning, the characters must be interpreted.

Otherwise the phenetic groupings will not accurately reflect evolution. This is evident in the grouping by Wake and Özeti (1969) of *Salamandrina* with *Salamandra* and *Chioglossa*. The protrusible tongue of the former is all but certainly convergently (and only superficially) similar to that of the salamandrines. The frontosquamosal arch, cranial structure, separation of a *rectus abdominis profundus*, lack of second basibranchial, high neural crests with robust capping plates, structure of the *dorsalis trunci* and *subvertebralis*, and the presence of long ribs all indicate the close relationship of *Salamandrina* with *Pleurodeles* and *Tylototriton*. As recognized by almost all previous workers (Boulenger 1882, Cope 1889, Dunn 1926, Bolkay 1928, Herre 1935b, von Wahlert 1953, and Thorn 1968), "*Salamandrina* is merely a European newt lacking the fifth toe" (Noble 1931, p. 475) and closely allied to *Pleurodeles* and *Tylototriton*.

I separate the Salamandridae into two subfamilies, the Salamandrinae and Pleurodelinae, which are distinct in terms of shared and derived features. The Salamandrinae consists of only *Salamandra* and *Chioglossa*, and differs from the newts in terms of cranial anatomy, the vertebral column, and trunk musculature. The subfamilies seem to share a sister-group relationship (see Fig. 101) of descent from a common ancestor. Each lineage subsequently became divergently specialized, but salamandrines retained the majority of the relatively more primitive character states. Salamandrines and the *Pleurodeles* group (tribe Pleurodelini) share unfused premaxillae in the adult, some members with two pairs of radii on the first basibranchial, some members with at least partial differentiation of the *rectus abdominis*, and similar

courtship patterns. To these probably primitive features may be added, questionably, the elongate, somewhat divergent anterior flexures in the *dorsalis trunci* of *Salamandra* and *Pleurodeles*.

Salamandrines are primitive as regards the posterior flexures of the subvertebral musculature, lack of a frontosquamosal arch, structure of the auditory apparatus (see Reed 1920, Monath 1965), and general flexibility and structure of the snout. The *Pleurodeles* group is probably primitive as regards the free *rectus abdominis profundus* in *Salamandrina* and *Tylototriton*.

I subdivide the Pleurodelinae into two tribes: the Pleurodelini for *Pleurodeles*, *Salamandrina*, and *Tylototriton*, and the Triturini for the remainder of the newts (see Table 3). The relationships of these tribes are shown in the tentative cladogram of Figure 101. The triturines are derived with respect to the *Pleurodeles* group. They have (excepting *Taricha*) lost the second pair of radii from the first basibranchial, the premaxilla is a single element, their patterns of courtship are evidently highly modified (see data in Salthe 1967), and their trunk musculature is derived. Unity of the tribe is also shown by the presence of tetrodotoxin in many of the included genera (see Brodie et al. 1974): *Notophthalmus*, *Taricha*, *Cynops*, and *Paramesotriton*.

In light of studies tending to indicate close relationships within the Asian species (except *Tylototriton*) on the one hand, and between *Notophthalmus* and *Taricha* on the other, and in the absence of positive controverting evidence, these may be considered to form

natural groups. Özeti and Wake (1969) showed similarities in the hyobranchial apparatus within the two, and courtship data seem to indicate unity of the North American and Asian species into two generic groups: the *Notophthalmus* group (with *Notophthalmus* and *Taricha*) and the *Cynops* group (*Cynops*, *Paramesotriton*, *Pachytriton*, and *Hypselotriton*). Tihen (1974) has described fossils that indicate close relationship between *Notophthalmus* and *Taricha*. The trunk musculature of *Cynops* and *Paramesotriton* is similar (see above) and, although somewhat different, the musculature of *Notophthalmus* is derivable from that of *Taricha* by paedomorphosis.

The exact relationships and sequences of splitting of the *Cynops* and *Notophthalmus* groups are uncertain. Courtship data (with capture in the North American newts), the strong frontosquamosal arch in the *Notophthalmus* group, and the retention of a second pair of radii in *Taricha* tend to indicate that the North American species are more primitive. Included in the *Cynops* group are members with great variability in the development of the frontosquamosal arch (Chang and Boring 1935). As this reduction seems, in this case, to be secondary, the condition in the *Notophthalmus* group is more primitive. Courtship in the *Cynops* group resembles that of *Triturus*, with no capture by the males (see Salthe 1967). I suggest that the *Notophthalmus* group split from the stock that eventually gave rise to *Triturus* and its allies prior to the divergence of the *Cynops* group (see Fig. 101), but this is tentative.

The remaining European newts can be separated into two apomorphic generic groups: the *Triturus* group (with *Triturus* and *Neurergus*

included) and the *Euproctus* group (only *Euproctus*). *Neurergus* is very close to *Triturus*, as recognized ever since Cope (1862) proposed the former genus (see Wolterstorff 1926, Bolkay 1928, Herre 1932, Özeti and Wake 1969, Wake and Özeti 1969). I show the *Triturus* and *Euproctus* groups as the most derived of the Salamandridae and sharing a sister-group relationship (Fig. 101). Both groups show variability and tendency to loss of the frontosquamosal arch. In view of the likelihood of the primitive position of the Pleurodelini within the Pleurodelinae, it seems that those newts lacking a fully bony arch have undergone secondary loss, as is corroborated by the presence of a ligamentous arch as a replacement (except, apparently, in *Triturus cristatus*). Courtship data also indicate the derived nature of these two groups (see Salthe 1967), with *Euproctus* being perhaps derivable from *Triturus* in this regard.

Nevertheless, the relationships of these two generic groups is tentative. Herre (1935b) suggested that *Euproctus* was most closely related to the Asian *Pachytriton*. In this regard, it is noteworthy that of the six different clustering analyses run by Wake and Özeti (1969) all produced a phenogram showing *Pachytriton* and *Euproctus* as the most similar, and the position of *Euproctus* remains uncertain. My proposed classification of the Salamandridae is given in Table 3.

The relationships of the Salamandridae to the other families have long been uncertain. Cope (1889) considered them to have been derived from anbystomatid ancestry, whereas Dunn (1926) suggested they were structurally ancestral to plethodontids. Noble (1931)

followed Dunn, also noting that the "body musculature" of *Salamandra* was similar to that of plethodontids and deriving salamandrids directly from hynobiids. Herre (1935b) derived salamandrids and plethodontids from a common ancestor.

The close relationship of plethodontids and salamandrids is presently rejected (see Laurent 1947, Larsen 1963, Regal 1966, Wake 1966). As the relationship was largely, or exclusively, based on the disposition of the vomerine and parasphenoid teeth, rejection was proper. However, my studies demonstrate that there is, in fact, a close relationship between salamandrids and plethodontids, although not precisely of the sort envisaged by earlier workers.

Salamandra shows certain resemblances to plethodontids. As shown above, the opisthocoelous condition is owing to posterior pull on each posterior cotyle. Plethodontids have posterior flexures or posterior basapophyseal muscles, *Salamandra* retains posterior flexures, and all salamandrids and certain plethodontids are opisthocoelous. The premaxilla develops as a fused element in embryonic *Salamandra* (personal observation) and this has been shown to be the primitive form of development in plethodontids (see Wake 1966). Certain newts (*Tylototriton* and *Salamandrina*) as well as *Chioglossa* retain a free *rectus abdominis profundus* extending from hyobranchium to pelvis, which is shared with plethodontids. In addition, the cranium of salamandrids is readily derivable from that of *Plethodon*, except as regards the vomer and auditory apparatus (see Reed 1920, Monath 1965).

Schaeffer's (1941) study of the tarsus in amphibians and reptiles shows similarity between this unit in plethodontids and salamandrids

that is not shared with other urodeles. Although he claimed that the tarsus of *Salamandra* was more derived than that of the newts, this cannot be supported. *Salamandra* retains four elements in the tarsale series, whereas the newts (e.g., *Triturus*) have only three. The tarsus of salamandrids (e.g., *Salamandra*) and plethodontids (e.g., *Desmognathus*, see Schaeffer 1941, fig. 2) is composed of the same number and kinds of elements, situated in the same way. In both families, tarsale one and tarsale two have fused into a single transverse unit supporting the first and second digits. By contrast, ambystomatids have a longitudinally elongate element formed by fusion of the first centrale and first tarsale in this position.

Lombard (1977) divided the inner ears in the Caudata into two sorts, "aquatic" and "terrestrial," noting that only plethodontids and salamandrids have a "terrestrial" kind of inner ear. He also stated (p. 130) that the inner ear of these two families is "the most paedomorphic and the most elaborate and novel" amongst the urodeles, and that "the novel aspects [of the inner ear] found in the two groups are unique in vertebrates" (p. 131). Although, citing Edwards (1976), Lombard concluded that these unique resemblances were convergently developed in plethodontids and salamandrids, in light of the other evidences they are probably owing to apomorphy.

I suggest that the most reasonable theory to account for these resemblances is that plethodontids and salamandrids have descended from a common ancestor, with each lineage having become divergently adapted. The two families share several apomorphic character states, whereas the states shared by plethodontids and ambystomatids are

primitive with respect to non-cryptobranchoid salamanders. Although this suggestion of relationship (see Fig. 103) may seem a radical and/or retrogressive step, it does not differ greatly from ideas presently accepted. That is, it is here admitted that plethodontids and ambystomatids are closely related, the change comes in also relating the former to salamandrids. There is good evidence for this latter contention (see above) and I group the Salamandridae with the Plethodontidae (see below and Table 4), although in separate superfamilies, not in an attempt to depreciate the resemblances of plethodontids and ambystomatids, but in order to emphasize the derived character states rather than the primitive. Plethodontids and salamandrids (as well as proteoids and sirenids) are members of a group having undergone a fundamental adaptive shift in the locomotory system.

xi) Sirenidae Gray 1825

CONTENT. *Siren* Linnaeus 1766, *Pseudobranchius* Gray 1825, *Habrosaurus* Gilmore 1928.

FOSSIL RECORD. Estes (1964, 1965b) described the earliest known sirenid, *Habrosaurus dilatus* Gilmore 1928, in detail. This species is known from the Upper Cretaceous and Paleocene of central North America (Estes 1964, 1976, Estes et al. 1969, Fox 1972), and includes the species *Adelphesiren olivae*, named by Goin and Auffenberg (1958) from the Lance Formation, as a junior synonym. Estes (1964) assigned ceratobranchials, dentaries, premaxillae, maxillae, palatal tooth

plates, atlantes, and numerous trunk vertebrae from the Lance Formation (Upper Cretaceous, Wyoming) to *Habrosaurus*.

Dentaries of *Habrosaurus* are similar in overall shape to those of *Siren*, but whereas those of living sirenids have teeth only on the coronoid, *Habrosaurus* retains teeth on the dentary. These are robust, non-pedicellate, and provided with flat, crushing crowns. Also unlike Recent sirenids, *Habrosaurus* has toothed maxillae and premaxillae. In *Siren*, maxillae are reduced to tiny slivers of bone (see Larsen 1963) and the premaxillae are delicate and edentulate.

Atlantes assigned to *Habrosaurus* differ from those of *Siren* in their possession of a broad, blunt odontoid process, but this is a matter of degree (compare Fig. 11, Estes 1964, fig. 37). Vertebrae (Estes 1964, pp. 74-77) have the relatively high neural crests and aliform processes that are also diagnostic of *Siren* and *Pseudobranchius*. The genera differ in "the invariable presence in [*Habrosaurus*] . . . of well-developed basapophyses on the ventral border of the anterior cotyle, and the lack of high, fin-like neural spine [= neural crest] and aliform processes" (Estes 1964, p. 79). The latter part of the quotation does not mean that aliform processes and neural crests are lacking, but that they are lower than in living sirenids. Estes (1964, p. 79) suggested that either the basapophyses of *Habrosaurus* are incorporated into the ventral lamellae in *Siren*, or "the extensions of the transverse processes replace, rather than obscure, the basapophyses."

Although either interpretation is possible, my study of the trunk musculature indicates that the "basapophyses" of *Habrosaurus* are secondary derivations from the ventral lamellae of the transverse

processes. The muscle projecting from the ventral lamella in *Siren* is not homologous to the anterior basapophyseal muscles of other salamanders (see above), indicating that the structures of *Habrosaurus* are probably not true basapophyses. If this is so, *Habrosaurus* cannot form an ancestor-descendant relationship with *Siren* or *Pseudobranchius*, but must represent an early, divergent lineage. This conclusion is partially corroborated by the massive dental apparatus of *Habrosaurus*.

Except for a Paleocene record (Estes 1976) of *Habrosaurus*, all Tertiary fossil sirenids are referable to the living genera. Goin and Auffenberg (1955, 1957) studied the known fossil material and named several new species. They recognized *Siren dunni* from the middle Eocene of Wyoming, *S. hesterna* from the lower Miocene of Florida (additional specimens were reported by Estes 1963), and *S. simpsoni* from the Pliocene of Florida. Holman (1966) noted material referred to *Siren* species from Miocene rocks in Texas. In addition to these fossil species, *Siren lacertina* is known from the Pleistocene of Florida (Goin and Auffenberg 1955, Lynch 1965).

Two fossil species of *Pseudobranchius* were named by Goin and Auffenberg (1955): *P. robustus* from the Pleistocene and *P. vetustus* from the Pliocene of Florida. Holman (1962) reported additional specimens of *P. robustus* from the Pleistocene of Florida and Lynch (1965) referred material from the same age to *Pseudobranchius* cf. *robustus*, noting that, as there is overlap with the Recent *P. striatus*, the species *P. robustus* may not be valid. The fossil material of *Siren* and *Pseudobranchius* consists of vertebrae and is of interest only in that it documents paleozoogeographic distributions. It provides no information as to the relationships of the family.

RELATIONSHIPS. The origins and relationships of sirenids have been uncertain. Cope (1889) classified the family in a distinct order, Trachystomata, which he indicated as being derived from the Urodela. Goin and Goin (1971) attempted to reinstate this order, as it is claimed to be "sharply distinct" from the other families of salamanders. However, in light of the numerous and detailed resemblances between sirenids and other urodeles, and because no data in support of the contention have been provided, this step has not been followed (see also Estes 1965b).

Dunn (1922) noted that the relationships of *Siren* and *Pseudobranchius* were unknown. Noble (1931) continued to classify them in a separate suborder, but observed that their lack of cloacal glands indicated external fertilization and noted the possibility of derivation from hynobiids. In his figure 145, however, tentative relationship to ambystomatids is indicated. Herre (1935b) argued for a salamandrid ancestry. Reed (1920) considered the auditory apparatus to relate sirenids to the salamandrid newts, whereas Larsen (1963) tentatively derived the family from a plethodontid ancestor.

As can be seen, almost every possibility has been suggested and, at present, sirenids are classified in a separate suborder of uncertain affinities (Regal 1966, Wake 1966, Edwards 1976). Most recently, Putnam (1976) suggested that sirenids are more primitive than crypto-branchoids. This was based on the claimed similarity between the hearts of lungfish and sirenids. What this contention overlooks is that lungfish and salamanders are not at all related, that sirenids and lungfish share similar sorts of habitats, and that all other

features of sirenids argue against the conclusion. The resemblances in the heart of sirenids and lungfish are owing solely to adaptive convergence and indicate nothing about the relationships of sirenids.

Previous workers have commented on the similarities between sirenids and the salamandrid newts, and it is here argued that sirenids are derived from a salamandrid ancestor. Noble (1931) noted the marked lateral positioning of the olfactory lobes in *Siren* and newts, presumably a derived condition. Reed (1920) and Herre (1935b) believed sirenids to be derived from salamandrids.

The otic region is of major interest (see Kingsbury and Reed 1909, Reed 1920, Larsen 1963, Monath 1965). The middle ear of *Siren* is constructed in such a way as to indicate derivation from a normally metamorphosing ancestor that had completely lost a free, functional columella, as is the case in newts. Unlike all other paedogenic salamanders, sirenids lack the *stylus columella*. The operculum remains as a free element in the *fenestra ovalis* and maintains a connection to the *levator scapulae*. This is remarkably similar to the situation in newts. Other larval aquatic salamanders of more primitive structure have the columella as the mobile unit in the middle ear, serving to transmit vibrations from the suspensorium (e.g., proteids, amphiumids, and cryptobranchids). In *Siren* the operculum has been secondarily modified for fully aquatic sound reception (see Kingsbury and Reed 1909), with a connection extending between it and the hyobranchium.

Estes (1964, 1965b) noted the marked resemblance between newts and sirenids in the high neural crests and aliform processes of the vertebrae. Aliform processes are not unique to sirenids (contra

Auffenberg 1959), but a derived character shared with newts. Edwards' (1976) descriptions of the patterns of spinal nerve exits show unique identity in sirenids and salamandrids (with all nerves usually exiting intravertebrally). Estes (1964, p. 79) remarked that the arrangement of the vomerine teeth in *Habrosaurus* "closely resembles the pattern of vomerine teeth seen in [the] Salamandridae, and may indicate relationship to the Salamandroidea." Sirenid cranial anatomy is of larval aspect (see Larsen 1963, Estes 1965b) and, although modified, does not debar a salamandrid ancestry.

My dissections show detailed and marked similarity in trunk musculature between sirenids and newts (see descriptions above). It is evident that *Siren* has become secondarily adapted to aquatic life, developing musculature for anguilliform locomotion in a manner convergent with, but quite different from, *Amphiuma*. The structure of the vertebral column and associated musculature of *Siren* demands derivation from a fully opisthocoelous ancestor with greatly simplified trunk musculature. Early derivation from primitive salamander stock (Cryptobranchioidea and Ambystomatoidea) is forbidden by these observations.

The epaxial myomeres are reminiscent of the condition in newts, and are probably only derivable from such an opisthocoelous ancestor. Hyperapophyseal muscles are like those of newts having high neural crests and aliform hyperapophyses. The subvertebral musculature is readily derivable from that of newts (e.g., *Notophthalmus*), but not from any more primitive ancestor (compare descriptions and figures of hynobiids, ambystomatids, and plethodontids). Superficially, the

anterior projections from the ventral lamellae of *Siren* appear to be homologous to anterior basapophyses, but the structure of the associated septa and muscle fibers and the absence of posterior flexures show that no homology exists between them and the true anterior basapophyses of cryptobranchoids and ambystomatoids.

In *Siren* a strap-like septum extends forward from each anterior projection of the ventral lamella. Muscle fibers fan anteriorly from these septa onto the ventral surfaces of the next anterior ventral lamellae (see Fig. 87). By contrast, in those species possessed of true anterior basapophyses a more or less vertical septum extends forward and another septum backward from each basapophysis. The anterior septum, and its associated musculature, forms the anterior basapophyseal muscle, whereas the posterior septum forms part of the posterior (or transverse process) flexure. The anterior basapophyseal muscle is, in addition, associated with the lateral surface of the centrum and not with the transverse process.

This ventral lamellar muscle of *Siren* is, however, readily derivable from the pattern exhibited by newts (e.g., *Notophthalmus*) that have well-developed, plate-like ventral lamellae on each transverse process. All that is necessary is that fibers inserting on the anterior edge of one lamella come to extend forward and attach to the ventral surface of the next anterior ventral lamella.

The *transversus* of sirenids is, seemingly, of unique structure, its dorsal portion extending into the *subvertebralis* and attaching to the lateral edges of the ventral lamellae and centra by tough fascia. In newts the *transversus* attaches to the centra, extending under the

subvertebralis and ventral lamellae. In *Paramesotriton* (see Fig. 77) the *transversus* also attaches to the ventral lamellae in places, but the *transversus* is still located ventral to the *subvertebralis*. The situation in the two families would, therefore, seem to be quite different. The more ventral part of the *subvertebralis* in *Siren*, however, is a secondary development owing to the neomorphic ventral lamellar muscles. The *subvertebralis* proper remains dorsal to the ventral origins of the *transversus*, as in *Paramesotriton* and other newts.

The lateral abdominal musculature of *Siren* consists of four lateral layers and a simple ventral *rectus abdominis*. This condition is explainable as a neotenic adaptation for aquatic, anguilliform locomotion and is closely approached by newts such as *Notophthalmus* and *Triturus cristatus*.

Although the method of reproduction is not known, the lack of spermathecae in female sirenids has usually been interpreted as evidence for external fertilization, as in cryptobranchoids (Noble 1931). However, owing to the fact that the eggs of *Siren* and *Pseudobranchius* "are deposited either in small groups or singly and not enclosed within the common envelope of jelly so characteristic of the Hynobiidae" (Boyden and Noble 1933, p. 3), it is probable that fertilization is internal. This sort of egg-laying recalls that of the salamandrids and "the eggs resemble those of some newts more than they do those of any other salamander" (Boyden and Noble 1933, p. 3). In the live-bearing *Salamandra* sperm enters directly into the oviducts to fertilize the eggs and perhaps sirenids have a similar sort of fertilization. Boyden and Noble (1933) note the possibility that the cloacal glands of sirenids have been lost owing to paedomorphosis.

The high chromosome number of sirenids (*Pseudobranchius* with a count of $n=32$; *Siren lacertina*, $n=26$; and *S. intermedia*, $n=21$; see Morescalchi 1975) has been used as evidence for a more primitive status than is here argued (Morescalchi 1975, Edwards 1976). However, Morescalchi and Olmo (1974) demonstrate the possibility that sirenids are tetraploid and such an interpretation fits much better with the other anatomical evidences. As noted by Morescalchi (1973), karyology must be considered together with data from other systems and not as an infallible guide to relationships (see also above). There is a further, but very tenuous, piece of evidence from karyology. In *Siren intermedia* and *Triturus helveticus* it is known that only the female undergoes recombination (Watson and Callan 1963, Leon and Kezer 1974), perhaps indicating affinity of their two families.

It is, therefore, reasonable to conclude that sirenids are derivable from some fully opisthocoelous ancestor, which had lost complexity in the *subvertebralis* and *dorsalis trunci*. There are few, if any, features debarring extant newts from a position of structural ancestry. Although contemporaneous species cannot, of course, form any sort of an ancestor-descendant relationship, it is likely that if known the ancestor of the Sirenidae would be classified as an apomorphic salamandrid without modifying the definition of the Salamandridae. In order to reflect this relationship (see Fig. 103), I classify the Sirenidae with the Salamandridae in the superfamily Salamandroidea.

xii) Prosirenidae Estes 1969

CONTENT. *Prosiren* Goin and Auffenberg 1958, *Albanerpeton* Estes and Hoffstetter 1976, ?*Ramonellus* Nevo and Estes 1969.

OCCURRENCES AND RELATIONSHIPS. *Prosiren elinorae* is known from the Lower Cretaceous Trinity Formation of Texas, where it is represented by atlantes, vertebrae, premaxillae, dentaries, and a single humerus (see Estes 1969c, figs. 1 and 2). It was originally described as a sirenid by Goin and Auffenberg (1958), but Estes (1969c) showed that it was referable to no extant family. The jaw elements are of the same sort as those assigned by Estes (1964) to *Prodesmodon* and were used as the basis for uniting *Prosiren* and *Prodesmodon* in a new family, the Prosirenidae (Estes 1969c). The supposed presence of genera with different sorts of vertebrae (*Prosiren* being amphicoelous and *Prodesmodon* opisthocoelous) was held to document the relationship of plethodontids and ambystomatids, with which the Prosirenidae were placed in the Ambystomatoidea.

Nevo and Estes (1969) subsequently added *Ramonellus longispinus* from the Lower Cretaceous of Israel to the Prosirenidae, although questionably. *Albanerpeton inexpectatum*, from the Miocene of France, is represented by extensive vertebral, appendicular, and cranial material. This has been described by Estes and Hoffstetter (1976), who note that an atlas from the Jurassic of Europe described by Seiffert (1969) is also from a prosirenid. *Albanerpeton* has the unique dentaries, maxillae, premaxillae, and humeri of *Prosiren*, as well as comparable vertebrae, although there is developed an "atlas-axis" complex unknown in other salamanders.

Atlantes, premaxillae, maxillae, dentaries, and cranial roofing bones very like those of *Albanerpeton* are known from the Upper Milk River Formation (Upper Cretaceous), Alberta. Jaw material previously called *Prodesmodon* is known from many Upper Cretaceous formations in North America (Estes 1964, 1969c, Estes et al. 1969, Sahni 1972, Fox 1972, 1976, Naylor 1978a), as well as from the Paleocene of Alberta (Fox pers. comm.) and Montana (Van Valen and Sloan 1965). I show elsewhere that this material is not properly referred to *Prodesmodon copei*, which is based on a vertebra (see Naylor 1978a). The jaw material is properly referred to *Albanerpeton* or a new genus near *Albanerpeton*, as shown by the atlantes from the Upper Milk River Formation. Estes and Hoffstetter (1976) provide figures and descriptions of the French prosirenid material.

The proper relationships of the Prosirenidae are uncertain. If they are salamanders, they are closest structurally to cryptobranchoids. The vertebrae apparently lack foramina for spinal nerves, the post-dentary bones are not fused together, and anterior basapophyses are present (although Estes and Hoffstetter [1976] note that weak posterior basapophyses are also present on some vertebrae of *Albanerpeton*).

The cranial material and "atlas-axis" complex are unique amongst salamanders, although the vertebrae appear to be similar to those of urodeles. The dentaries are small, but very robust and provided with strong non-pedicellate teeth, which apparently lack basal pits for a replacement series. There is a unique symphyseal joint of a sort unknown in other salamanders (see Estes and Hoffstetter 1976). The articular surface for the quadrate faces posteriorly from the lower jaw.

The skull of *Albanerpeton* as reconstructed by Estes and Hoffstetter (1976, fig. 4) is high, and the roofing bones are also not of salamander aspect. The limb elements are unique in having well-ossified epiphyseal regions. The "atlas-axis" complex is formed of three vertebrae. The atlas is salamander-like anteriorly, but lacks posterior zygapophyses and has a concavity posteriorly for articulation with the "axis." This latter element is composed of two vertebrae fused together. The more anterior vertebra lacks a neural arch and forms a projection from the front of the third. Anterior zygapophyses are lacking from the third vertebra, the anterior of the neural arch being raised and expanded so as to abut the atlas (see Estes and Hoffstetter 1976, figs. 1 and 2, and accompanying descriptions).

If, in fact, prosirenids are salamanders, they are an early, divergent stock from very primitive ancestry. They are referable to no known superfamily, and I classify them *incertae sedis* within the Caudata (see Table 4).

xiii) Familial Synthesis

From the information and inferences on the inter- and intrafamilial relationships of the Caudata presented above, it is possible to integrate these conclusions into a coherent phylogenetic reconstruction and a classification that is consistent with it (see Figs. 102, 103, and 104, and Table 4). The order may be readily divided into two subdivisions, one primitive and one derived, and each characterized by its own trends. The more primitive division includes two superfamilies, Cryptobranchoidea and Ambystomatoidea, the cladistic relationships of which are diagrammed in Figure 102.

As has been long accepted (Dunn 1926, Noble 1931), the Cryptobranchioidea are held to be a natural and monophyletic group. The family Hynobiidae is the most phenetically primitive of living salamanders, probably representing structurally the ancestral salamanders in most features (see above). By variable processes of paedomorphosis and simplification and/or complication, the remainder of known fossil and Recent salamanders are derivable from hynobiids. The Cryptobranchidae include giant aquatic derivatives from hynobiid stock, retaining the same basic subvertebral and epaxial musculature and a larval system of lateral abdominal musculature. The skull has been remodelled, but within the limits of the basic hynobiid plan.

It is likely that all other salamanders (excepting prosirenids) form a monophyletic group (sensu Simpson 1961) derived from hynobiid or hynobiid-like ancestry. Shared-derived features include internal fertilization by means of a spermatophore (where known), elongate premaxillary spines, fusion of the angular and prearticular in the lower jaw, and a reduction in chromosomal number. The most primitive superfamily in this derived assemblage is the Ambystomatoidea (scapherpetontids, amphiumids, and ambystomatids). These salamanders show development of postatlantal intravertebral exits for spinal nerves, with a morphocline as follows (see also Edwards 1976);

1. Amphiumidae: the more posterior caudal vertebrae with intravertebral exits.
2. Scapherpetontidae: ?caudosacral and caudal vertebrae with intravertebral exits.
3. Dicamptodontinae: caudosacral and caudal vertebrae with intravertebral exits.

4. Ambystomatinae: except for those of the second cervical, all exits intravertebral.

This cline could well represent a phylogenetic event, with succeeding "escapes from specialization" (Maslin 1952). Evidence from other anatomical systems does not forbid such an interpretation.

I use a cladogram (Fig. 102) to diagram the relationships of ambystomatoids and cryptobranchoids, but rather than speaking of a sister-group relationship it is more proper to derive ambystomatids from hynobiid ancestry (see Fig. 104). As discussed above, the sequence of splitting of amphiumids and scapherpetontids from ambystomatid or pro-ambystomatid ancestry is uncertain. Amphiumids are represented as having diverged first on the basis of the patterns of spinal nerve exits and the presence of autapomorphies, perhaps indicating a longer time since separation. Nevertheless, this interpretation is tentative.

Ambystomatoids are structurally intermediate between cryptobranchoids and the more derived subdivision of the Caudata. They are defined by a combination of characters, rather than by one or two unique characters:

1. Internal fertilization where known.
2. Low chromosome number where known ($n=14$ or 13).
3. Fusion of angular and prearticular in lower jaw.
4. Elongation of premaxillary spines.
5. Retention of anterior basapophyseal trunk musculature.
6. Spinal nerves partially, but not totally, intravertebral in exit.

The position of the Prosirenidae is uncertain. If properly referred to the Caudata, the family is closest to the Cryptobranchoidea (see above) and I place them *incertae sedis* (and questionably) in the

primitive subdivision of the Caudata. Together the cryptobranchoids and ambystomatoids are considered to belong to a new suborder, defined on the pattern of trunk musculature. This suborder comprises the most primitive salamanders:

Order Caudata Oppel 1811

Suborder Archaeocaudata nov.

ETYMOLOGY. From the Greek ἀρχαῖος, meaning ancient, combined with the ordinal name Caudata, in reference to the suborder including the more primitive salamanders.

DIAGNOSIS. Salamanders with primitive trunk musculature, full development of anterior basapophyseal muscles and transverse process flexures subvertebrally, at least the second cervical lacking foramina for spinal nerves, and fully amphicoelous centra.

CONTENT. The families Hynobiidae, Cryptobranchidae, Scapherpetontidae, Amphiumidae, Ambystomatidae, and (questionably) Prosirenidae.

The families of the second suborder are divided into three superfamilies (see Fig. 103 and Table 4), as discussed above. These salamanders are derivable from ambystomatid or ambystomatid-like ancestry, with the Plethodontidae being the most primitive osteologically and myologically. Owing to basic trends continuing throughout the Caudata, it is difficult to produce a division of the families that holds for all anatomical systems. Cryptobranchoids, ambystomatids, plethodontids, salamandrids, and sirenids form a single morphocline

in many of their features (e.g., chromosomal number, trunk musculature, cranial structure, and osteology). Nevertheless, there is clear separation in terms of the trunk musculature and vertebral column, justifying separation. The second suborder includes the more derived salamanders (see also above):

Order Caudata Oppel 1811

Suborder Neocaudata nov.

ETYMOLOGY. From the Greek νέος, meaning new, combined with the ordinal name Caudata, in reference to the suborder including the more derived salamanders.

DIAGNOSIS. Salamanders having derived and simplified trunk musculature, with complete loss of anterior basapophyseal muscles and general reduction of the *subvertebralis*. All families include opisthocoelous species, or are derivable from opisthocoelous ancestry.

CONTENT. The families Proteidae, Batrachosauroididae, Plethodontidae, Salamandridae, and Sirenidae.

Each of the superfamilies in the Neocaudata (see Table 4) exhibits a combination of primitive (with respect to the Neocaudata) and derived character states, necessitating hypotheses of derivation from a common ancestor in all cases (see Fig. 103). Plethodontids are probably structurally most like the true ancestor of the suborder, although they differ in lacking lungs and the possession of tooth plates on the parasphenoid. The family bridges the structural gap between ambystomatids and the other families of the Neocaudata.

Exact cladistic relationships of the Proteoidea to the other superfamilies are not certain, as the structural evidence is equivocal. The lack of intravertebral exits for spinal nerves and the relatively high chromosomal number ($n=19$) might be taken as evidence that Proteoids are the most primitive neocaudates. However, such an hypothesis necessitates assuming convergent development of such exits and the low chromosomal number ($n=14$ in ambystomatids, amphiumids, and plethodontids) in the other families, which is probably less likely. It is most reasonable to assume secondary development of the higher chromosomal number and lack of intravertebral exits in proteoids. Nevertheless, proteoids are here considered to be early derivatives of neocaudate stock (see Figs. 103 and 104), based on their early fossil record and autapomorphies (see above).

There is good evidence that the Plethodontoidea and Salamandroidea share a common ancestor, probably most similar to plethodontines osteologically and myologically. The relationship is indicated by the patterns of spinal nerve exits (see also Edwards 1976), the low chromosomal number (sirenids probably being tetraploid), structure of the *subvertebralis* (see Fig. 90), retention in the more primitive salamandrids of a free *rectus abdominis profundus* also found in plethodontids (see above), and the structure of the tarsus (see Schaeffer 1941). Divergent specializations are shown in the vomerine teeth, condition of the lungs, and structure of the auditory region.

What I believe to be the most accurate phylogenetic representation of the history of the Caudata is given in Figure 104. Although cladograms were utilized in analysis of the relationships of certain

families, tribes, and genera, the cladistic approach has not proven useful or realistic in representing the overall phylogeny. The phylogenetic scheme is based on a variety of different characters (see above) and the characters are given differing weights from group to group. The phenetic approach was not used as there is not a sufficient number of characters that can be applied throughout the order. I do not believe that mere enumeration of features and/or cluster analysis is particularly useful for the Caudata.

The phylogenetic reconstruction is more realistic, more consistent with the phenetic and cladistic evidence, and provides a clearer visualization of the history of the Caudata than would a cladogram. Where reasonable, lineages have been shown as arising from known families, but in other cases families are shown as coming from a hypothetical common ancestor. This treatment is more practical than an attempt to force all families into a rigid cladistic framework, which would both distort relationships and claim less than it is possible to claim. By the same token, cladistic classification would lead to absurd results. For example, the Neocaudata would have to be considered a subfamily of the Ambystomatidae, which is not consistent with the realities of the evolutionary history (cladistic *and* patristic) of the Caudata. The evolutionary approach also ignores the proliferation of higher taxa demanded by cladistics. The classification (Table 4) is strictly evolutionary, with both aspects of the phylogenetic process clearly taken into account, and consistent with the phylogeny that I have constructed.

C. Biogeography

Although attention has been paid to the biogeography of certain of the families of salamanders, there has been little work on historical biogeography at the familial level. Savage (1960) and Wake (1966) deal with the ranges of the plethodontids and how these might have developed historically. Steward (1969) briefly discussed the effect of Pleistocene glaciation on the salamandrids of Europe and Tihen (1958) proposed a detailed theory of dispersal in the North American ambystomatids (see also above). Various workers have discussed the data available from the fossil record and its input into biogeographical reconstruction (see Estes 1965a, 1970, Tihen 1964). Dunn (1923b) considered the distribution of amphibians in order to test the theories of dispersal put forth by Matthew (1915) and Willis (1922). He found both views at variance with the facts.

Within the Caudata, centres of origin and subsequent patterns are difficult to elucidate owing to the early origins of the families, the lack of an adequate fossil record, the presently disjunct distributions, and the difficulty of interrelating the families. Nevertheless, historical biogeography of the salamanders is not completely hopeless. It is possible to draw certain tentative conclusions that are consistent with the known evidence.

The phylogenetic relationships of the eight Recent and two fossil families are relatively well understood (see above, also Fig. 104). Present ranges, ecological tolerances, habitat preference, and preferred climates are known. There is also fairly extensive information about paleogeography of the Northern Hemisphere (see

McKenna 1972, Russell 1975, Williams and Stelck 1975), with the most critical periods of time being the Cretaceous and early Tertiary. Various methods have been proposed that purport to enable the investigator to make inferences of past centres of evolution and paths of dispersal. There are perhaps seven such techniques, all of which are based on *a priori* assumptions, but some having a much more reasonable basis than others. The major problem is how to allow adequate testing of models outside of the framework of the assumptions. Certain of these biogeographic theories are proposed as general laws, when in fact they are not even adequate generalizations about specific groups.

Before considering salamanders specifically, it is necessary to discuss the different methods available. The most recently proposed approach is that of Crozait et al. (1974), which assumes that dispersal has *not* been important in the development of present patterns of distribution. It is believed that the main process is one whereby a "generalized," primitive stock inhabiting a wide area is passively split by geographical barriers so as to give rise to new species. If this is accepted, then a simple summation of the present distributions of a monophyletic taxon will give the area occupied by the ancestral species. Observations of Recent organisms, consideration of evolutionary theory, and study of the fossil record (e.g., horses) show this method to be sterile and in major disagreement with the real evidence. Darlington (1957, p. 29) notes that it must be remembered *"that animals are living things, which are constantly evolving and multiplying in some places, spreading into other places, and dying out*

in others, and thus forming new geographical patterns. All zoogeographers [?should] know this, but not all think about it" (italics original). "Hologenesis" does not bear serious discussion and, although Croizat et al. (1974, p. 277) speak of formulating "explicit methods of statistical analysis [based on the concept of generalized tracks] that yield unambiguous and repeatable results," Dunn (1923b, p. 136) long before noted such "excellent examples of the use of statistics in support of conclusions to which they are irrelevant."

A second technique is the numerical (see Ross 1974). This assumes that the area having the greatest diversity of Recent species is the centre of origin for that particular taxon. This is doubtless true in certain cases, but it is to be demonstrated rather than assumed. The geographic technique is quite similar, assuming that the centre of dispersal is best determined by the geographic centre of the group's present range. As in the case of the numerical method, this can be a useful piece of evidence, but is to be demonstrated in each individual case.

The ecological approach states that if the direction of dispersal is known for a certain group any taxon in more or less direct ecological association will have the same direction of dispersal. This rule is probably usually true, but it is not of general applicability and the investigator must be certain that the ecological associations are not newly evolved (see Ross 1974 for discussion of these approaches).

According to the "age and area" hypothesis of Willis (1922, see also Hennig 1966, Brundin 1972b), the present distribution of the more primitive members of a group defines the centre of origin. Although

certain theoretical justifications can be made for this "rule" and it can, in some cases, be used to corroborate theories of centres of origin, it is to be demonstrated rather than accepted as a necessary truth. The biogeographic approach of Matthew (1915) and Darlington (1957, 1965) stands in direct opposition to the theory of Willis. According to Matthew, the distribution of the more derived members of a group will define the centre of origin of the group. The concept is that new, more "vigorous" species arise in an area and successively force the older, more primitive, members to the periphery. However, if we believe as seems reasonable that all species are adapted to their environments, there is no compelling reason to assume that either apomorphic or plesiomorphic species should be necessarily competitively superior. The concept, although doubtless true in certain cases, does not follow as a necessary consequence of observation or of theory.

These six methods are all based on one or more hard assumptions. Accepting the assumptions of any of these approaches and following the proper methodologies will produce answers. Unfortunately, the assumptions are not reasonable as general rules and are more likely to lead to error than to fact.

A final approach and, I would suggest, the only reasonable one is the evolutionary or phylogenetic. This method considers populations to be dynamic, evolutionary units and uses all possible lines of evidence in reconstructing past distributions and centres of origin. The evolutionary approach, like those noted above, is based on assumptions, but on assumptions that are demonstrably reasonable. It is accepted that organic evolution by means of natural selection is a

reality, that living species have ancestors potentially represented in the fossil record, and that dispersal is a fact. Various tools are available to the evolutionary biogeographer, including:

1. Neobiological: descriptive zoogeography,
ecological zoogeography,
comparative anatomy (leading to phylogenetic
conclusions).
2. Paleobiological: known first occurrences of taxa,
paleozoogeography,
comparative anatomy (leading to phylogenetic
conclusions).
3. Geological: continental drift and plate tectonics (allowing
for paleogeographical reconstructions),
paleoclimatology.

All of these tools are absolutely essential if biogeographic research is to be meaningful and productive. If one is limited (by necessity or choice) to neobiological analysis, the answers that are produced will have a lower degree of probability. If geological data are added to the neobiological data, the probability of approximation to reality increases. However, these geological data must be real and not manufactured so as to support some special theory (e.g., one cannot raft tectonic plates merely to support some theory of vicariance).

Finally, only the fossil record can show us where animals actually existed and at what times, as opposed to where a theory might demand that they be. For example, lacking the known fossil record, who could have determined the centre of origin of the mammalian perissodactyls

(rhinos, tapirs, and horses) to have been North America? Methods such as those utilizing "age and area" or "generalized tracks" are demonstrably inappropriate to situations in which centres of origin can be reasonably inferred and, therefore, especially to be avoided in situations lacking fossil data.

In attempting to elucidate the past histories of the families of salamanders it is necessary to start from what is known and proceed to what may be reasonably inferred. A brief summary of present ranges and known first occurrences is provided for each of the families:

Hynobiidae

1. Presently restricted to eastern Asia.
2. Questionably known from the Paleocene of Europe, otherwise there is no fossil record.

Cryptobranchidae

1. Disjunct distribution, two species in eastern Asia and one in eastern North America. From the fossil record and present ecological correlations it is probably to be concluded that this does not represent a relict distribution, but one of shifting ranges, moving through time as the environment changed.

2. First known from the Paleocene of North America (jaw material, Ravenscrag Formation, Saskatchewan), and also from the Oligocene through Pliocene of western Europe and the Miocene and Pliocene of eastern North America (Westphal 1958, Meszoely 1966).

Amphiumidae

1. Found only in the southeastern United States.

2. First known from the Upper Cretaceous and Paleocene of the western interior of North America (Estes 1969b).

Scapherpetontidae

1. Known from the Upper Cretaceous and Paleocene of the western interior of North America (Estes 1969a, 1975, 1976, Estes et al. 1969).

Ambystomatidae

1. Found throughout most of North America.

2. First known from the Paleocene (Peabody 1954) and Eocene (Estes 1965b). It is possible to refer fossils from the Oligocene and Miocene of North America to extant species groups (see above).

Batrachosauroididae

1. Known from the Upper Cretaceous through to the Miocene in the western interior and southeastern parts of North America (see Estes 1969a, Naylor 1978a), and probably from the Paleocene and Eocene of western Europe (Herre 1935b, Estes et al. 1967, Naylor 1978a).

Proteidae

1. Found in the Appalachians of eastern North America and in western Yugoslavia.

2. First found in the Paleocene of Saskatchewan (Naylor 1978b), and also from the Oligocene of North America (Estes pers. comm.) and the Miocene of the Caucasus (Estes and Darevsky 1977).

Plethodontidae

1. Found in eastern and western North America, Central America, northern South America, and western Europe.

2. The fossil record is all but nonexistent, the family being first recorded by Pliocene trackways of *Batrachoseps* in California.

Salamandridae

1. Found in eastern and western North America, throughout Europe and in eastern Asia, as well as in the Middle East and northern Africa.

2. First known from the Paleocene of Europe (see Estes et al. 1967), then from the Oligocene and Miocene of North America and the Miocene of eastern Asia (Tihen 1974, Young 1965).

Sirenidae

1. Found in the southeastern United States.

2. Known first in the Upper Cretaceous of the western interior of North America (Estes 1964), with specimens referable to extant genera appearing in the early Tertiary of the same continent (Goin and Auffenberg 1955, 1957).

To this evidence must be added what has been reconstructed of the paleogeography of Cretaceous and early Tertiary time. Four areas are of importance in this regard: the De Geer land bridge connecting North America and Europe, the Turgai Straits separating Asia from Europe, the western interior seaway of North America, and Beringia (see Fig. 105). The De Geer land bridge allowed faunal exchange between Europe and North America until the middle Eocene, when the Atlantic Ocean disrupted it (McKenna 1972, Russell 1975). The Turgai Straits were present through almost all of the Cretaceous (Lillegraven 1974), allowed intermittent passage (at least of mammals) in the Paleocene and early Eocene, were fully developed by the middle Eocene, and then closed at the end of the Eocene to allow dispersal between Europe and Asia (Russell 1975). The area of Beringia was split by

the Arctic and Pacific oceans in the Late Jurassic and into Neocomian (Early Cretaceous) time. Thereafter Beringia served as an intermittent filter route for dispersal between Asia and North America (Lillegraven 1974, Russell 1975). Based on the fossil evidence and inference from the living families, it is likely that the Cretaceous and early Tertiary saw the development of the living groups of salamanders and their dispersal to the present ranges (see Tihen 1958, Estes 1965b, 1970).

In addition to this evidence, it is now possible to provide a reasonable phylogenetic scheme for all of the families of living salamanders (see above, also Fig. 104). These data together allow for the development of the following tentative proposal (see Fig. 105).

The Hynobiidae are the most primitive group of living salamanders, probably representative of the truly ancestral salamanders. If the Paleocene (*Wolterstorffiella* and *Geyeriella*) and Miocene (*Bargmannia*) fossils from Europe are correctly interpreted as hynobiids, the distribution of hynobiids was previously more extensive. Cryptobranchids, their closest living relatives, may have entered North America some time prior to the Tertiary, where they are represented by jaws from the Paleocene Ravenscrag Formation of Saskatchewan. Subsequently, the family is represented by specimens from the middle Tertiary of Europe and North America. Whether or not cryptobranchids originated in North America is uncertain, however. The European *Cryptobranchus scheuchzeri* is at least structurally ancestral to the east Asian *C. japonicus*, perhaps indicating dispersal westward across the area of the old Turgai Straits after the Eocene (see Westphal 1958). *C. alleganiensis* appears

to be a relatively recent, paedomorphic derivative from a similar stock. Although the present distribution of cryptobranchids could be interpreted as relict, it is more probable that this represents the end result of a history of shifting ranges and dispersal.

The Ambystomatoidea are probably a monophyletic stock (sensu Simpson 1961) derived from hynobiid ancestors that entered North America from Asia sometime in the Cretaceous, although this could perhaps be interpreted as a vicariance event from hynobiid stock already present in North America. The resultant pro-ambystomatids gave rise to amphiumids and scapherpetontids, these latter families being known from Late Cretaceous deposits from the old western shore of the interior seaway. Amphiumids managed subsequently to establish themselves in the southeast of the United States, but scapherpetontids went extinct. Meanwhile, the ambystomatids were evolving, with dicamptodontines segregating to the west of the Rocky Mountains and ambystomatines spreading more widely. The presence of the more primitive ambystomatids (*Dicamptodon*, *Rhyacotriton*, *Ambystomichnus*, *Ambystoma gracile*, *A. macrodactylum*, and *A. tihenii*) in western North America may indicate this to have been the centre of origin of the Ambystomatidae. More derived ambystomatines diverged from the older stock, perhaps in Appalachia, where the *Ambystoma maculatum* group is centred, as well as the more derived members of the genus. Dispersal into Mexico was probably the last event in the origin of the present distribution of the ambystomatines.

It is likely that the Ambystomatoidea have always been restricted to North America, where they gave rise to the neocaudate salamanders,

which came to be more widely dispersed. If, as seems likely, the Neocaudata are a monophyletic group of ambystomatoid ancestry, it is probable that these more derived salamanders originated in North America. The most structurally primitive neocaudates (plethodontids) are centred in North America, and the Batrachosauroididae are known from Upper Cretaceous deposits in the western interior of the same continent. Plethodontids probably arose from ancestors that, if known, would be readily classified as Ambystomatidae. Based on the present distribution of the most structurally primitive tribe, the Plethodontini, it would seem that the family was originally widely spread over North America. A major adaptive radiation resulted in both eastern and western North America: in the east the Euryciini evolved, eventually giving rise to the Desmognathini, while in the west the Bolitoglossini diverged and gave rise to representatives that eventually reached Europe (probably via Beringia) and also South America. The dating of these events is most uncertain, perhaps being Late Cretaceous or early Tertiary.

It is likely that the Salamandridae share a common ancestor with the Plethodontidae (see above), but the place of origin of the salamandrids is uncertain. The salamandrid radiation centred in Europe, which contains the most primitive living genera (within the Salamandrinae and Pleurodelini) and the earliest and most extensive fossil record of the family (see above, also Kuhn 1962, Estes et al. 1967, Estes and Hoffstetter 1976). From the European centre, it is likely that the Asian newts of the *Cynops* group, as well as the more primitive *Tylo to triton*, dispersed eastwards after the closing of the

Turgai Straits in the Eocene. The first known fossil newt (*Procyrops*) from eastern Asia is of Miocene age (Young 1965), and *Tylo to triton* and allied genera are known from the middle Tertiary of Europe (see above).

The North American newts perhaps entered via the De Geer land bridge prior to the middle Eocene, where they split into the two extant genera. These are known from the Oligocene and Miocene of North America (see Tihen 1974). On the other hand, if the *Notophthalmus* group is diphyletic, *Taricha* may have entered North America from Asia through Beringia.

As argued above (see also Fig. 104), it is likely that proteoids are relatively early derivatives from neocaudate stock. Batrachosauroidids are known from the Upper Cretaceous of the interior of North America, and the first proteids come from the Paleocene of Saskatchewan (Estes 1964, Naylor 1978a,b). The deltaic lowlands along the eastern shores of the western interior seaway (Estes et al. 1969, Estes and Berberian 1970) would have provided ideal habitats for the aquatic, larval representatives of these two families. Batrachosauroidids are also known from the Miocene of southern and southeastern North America (Estes 1969a), and the European representative of the family, *Palaeoproteus*, may have entered Europe via the De Geer bridge in the early Paleocene.

The Proteidae probably originated in North America, dispersing subsequently into Europe where they are presently represented by *Proteus*. It is probably not reasonable to call the present distribution of proteids relictual. Rather it is owing to a shifting of ranges and

continuous dispersal. If proteids are as close to batrachosauroidids as is here argued (see above), they probably originated some time in the latest Cretaceous or earliest Paleocene directly from the *Batrachosauroididae*.

The final family, the Sirenidae, has probably always been exclusively North American. The earliest representative of the family, *Habrosaurus*, from the Upper Cretaceous of the western interior of North America (Estes 1964, 1976) is extremely derived, thereby indicating an earlier origin for the family. If, as seems likely, sirenids originated from within the Salamandridae, this would place the origin of the latter considerably prior to the beginning of the Tertiary. Sirenids may well have originated along the western interior seaway of North America, dispersing eastwards as the oceans retreated after the end of the Cretaceous.

SUMMARY

1. The vertebral columns of representatives from each of the living families, including 18 species in 14 genera, are described in order to present the basic structural plans of each family. The descriptions are of the atlas, second cervical, a mid-trunk vertebra, the sacrum, and a haemal vertebra. Variation along the column of condyles and/or cotyles, hypapophyseal structures, neural arches, zygapophyses, and transverse processes are also provided. These raw data relate to:

- i) interpretation of the fossil record,
- ii) myological investigation of the trunk region,
- iii) phylogenetic interpretations of the order.

2. Detailed descriptions and figures of the axial musculature in the midtrunk region of representatives from all of the extant families, including 61 species in 37 genera, are provided. This documents a major amount of diversity and interfamilial variation in all portions of the axial musculature.

3. Studies of the vertebrae and trunk musculature demonstrate that certain features observed on fossil vertebrae are of important taxonomic significance. These include: aliform processes, anterior basapophyses, and posterior basapophyses. Other features are of more minor importance.

4. Dissections of the trunk musculature of salamanders, as well as of certain snakes and lizards, allow for the proposal of more detailed

hypotheses on the origin and significance of the ball-and-socket intercentral joint. This joint serves primarily as a strengthening device, preventing dislocation of the intercentral joints.

5. Amphicoelous salamanders are aquatic, of small size, possessed of larger amounts of trunk musculature distal to the column, and/or possessed of complex flexures that concentrate force away from the column. These factors indicate reduced strain intercentrally.

6. Opisthocoelous salamanders have a more intimate association of musculature with the vertebrae and have reduced the complexity of the *subvertebralis* and (to a lesser extent) the *dorsalis trunci*. This produces increased intercentral strain.

7. The majority of opisthocoelous salamanders do not have a true ball-and-socket joint. The joints are cup-in-cup, clearly indicating the anti-dislocation function (see Fig. 93) and that the joint is not primarily serving to increase flexibility.

8. The end of the centrum developing the "ball" depends on Fick's rule. If the pull is posterior and concentrated on the rear cotyle, then opisthocoely develops (plethodontids, batrachosauroidids, and salamandrids). If the pull is anterior and on the forward cotyle, then procoely develops (snakes and lizards).

9. Elongate transverse processes are hypothesized to be owing to two factors:

i) they are possible owing to the buccal pump method of lung ventilation,

ii) they are present because they serve as rigid parts of the myosepta, being points of attachment for intervertebral muscle fibers, probably owing to the necessity for the rapid initiation of locomotion in prey capture and predator escape.

10. Bicipital rib-bearers do not develop in order to counteract the pull of gravity on the viscera (compare lizards and frogs), but because of locomotory constraints. The rib-bearers and ribs are integral parts of the myoseptal system.

11. A discussion of biological systematics is provided, in which it is concluded that:

i) the study of function is necessary in phylogenetic analysis,

ii) the premises of both phenetic and cladistic approaches to taxonomy and phylogenetic analysis are to be rejected,

iii) the evolutionary approach to systematics is accepted as the most reasonable.

12. A series of principles to be used in phylogenetic analysis are proposed, what constitutes "good" phylogenetic characters is considered, and concepts pertinent to systematic study are discussed (i.e., homology, parsimony, primitiveness, and the biogenetic "law").

13. A series of principles to be used in biological classification is

provided and defended. Evolutionary classification is accepted as the most reasonable approach to ordering the organisms.

14. A brief history of concepts of classification of salamanders since the time of Linnaeus is provided, in order to show the historical development of present ideas and to illustrate the necessary subjective component in classification. Classification is partly science and partly art, by necessity.

15. Hynobiids and cryptobranchids are accepted as closely related, representative of the most primitive living salamanders, and to be classified in the superfamily Cryptobranchoidea.

16. Primitive characters retained by hynobiids include: paired premaxillae with short nasal spines, retention of lacrimal and septomaxillary, retention of angular and prearticular in lower jaw, columella and operculum in middle ear, external fertilization, retention of second epibranchials in the adult hyobranchium, relatively long and low vertebrae, centra amphicoelous, appressed rib-bearers, postatlantal spinal nerves exiting intervertebrally, *subvertebralis* with anterior basapophyseal musculature and associated transverse process flexures, *rectus abdominus* divided into the *r. a. superficialis* and a free *r. a. profundus*, and only two layers of lateral abdominal musculature in most metamorphosed adults.

17. Scapherpetontids, amphiumids, and ambystomatids are to be grouped in the superfamily Ambystomatoidea, which evolved from hynobiid or

hynobiid-like ancestry. The superfamily is united by a series of characters: internal fertilization by means of a spermatophore (where known); fusion of angular and prearticular; some, but not all, post-atlantal spinal nerves exiting intravertebrally; and retention of the primitive sort of trunk musculature.

18. *Rhyacotriton* and *Dicamptodon* are grouped into a single subfamily, the Dicamptodontinae, as sharing unique features, both primitive and derived with respect to ambystomatines. These include: separate prootic, foetalized trunk vertebrae, pattern of exits of spinal nerves, structure of the *dorsalis trunci*, and structure of the lateral abdominal musculature.

19. The following modification to Tihen's (1958) species groups of the genus *Ambystoma* are suggested:

- i) *A. macrodactylum*, *A. gracile*, and probably *A. tihenii* are placed in a new species group, as being the most primitive *Ambystoma*, perhaps inhabiting the ancestral area of the Ambystomatinae.
- ii) The *A. tigrinum* species group is held to also include Tihen's *A. mexicanum* species group and the subgenus *Bathysiredon*.
- iii) Continued usage of the subgenera *Ambystoma* and *Linguaelapsus* is rejected, the latter becoming the *A. cingulatum* species group.
- iv) The *A. tigrinum* complex of species is the most highly derived (paedomorphic) of the genus *Ambystoma*.

v) The *A. maculatum* species group is derived from the *A.*

macrodactylum group and, in turn, gave rise to the *A. opacum*,
A. cingulatum, and *A. tigrinum* species groups.

vi) *Rhyacosiredon* is the most derived member of the Ambystomatidae,
being derived via paedomorphosis from the *A. tigrinum* group.

20. Derivation of plethodontids from ambystomatid ancestry is accepted, but an argument for close relationship to the salamandrids is also made, the two families probably sharing a "sister-group" relationship. This is indicated by the pattern of spinal nerve exits, the structure of the *subvertebralis* and lateral abdominal musculature, the structure of the tarsus, and the development of the premaxillae.

21. It is tentatively suggested that the most primitive pattern of reproduction within the Plethodontidae is that seen in the Plethodontinae, which lay terrestrial eggs and generally brood them. This means that the aquatic larval stage of the Desmognathinae is secondary, as is all but certainly the case in *Hemidactylum*.

22. *Hemidactylum* and *Batrachoseps* are included in the tribe Plethodontini, along with *Plethodon*, *Aneides*, and *Ensatina*. The Bolitoglossini then includes *Hydromantes* and the supergenus *Bolitoglossa*. These two tribes have a sister-group relationship and are classified in the subfamily Plethodontinae.

23. Wake's (1966) Hemidactyliini is here termed the Euryciini, owing to removal of *Hemidactylum*. A tribe Desmognathini is recognized to

include *Desmognathus*, *Leurognathus*, and *Phaeognathus*. These two tribes share a sister-group relationship and are included in the Desmognathinae, which shares a common ancestry with the Plethodontinae.

24. Continued recognition of *Leurognathus* as a genus distinct from *Desmognathus* is questioned, but no formal taxonomic change is proposed.

25. Close relationship of *Proteus* and *Necturus* is justified, the arguments of Hecht and Edwards (1976) being considered, but not accepted. Proteids also share a derived condition of the *subvertebralis*, which further justifies an hypothesis of monophyly.

26. Proteids and batrachosauroidids are considered to be closely related and to be properly classified in the superfamily Proteoidea. Estes' (1975) suggestions are, therefore, accepted and further supporting evidence is proposed. The two families may even form an ancestor-descendant relationship.

27. Proteoids are most closely related to plethodontoids and salamandroids, being probably derived from the primitive stock that gave rise to these two latter groups. Under this interpretation the absence of postatlantal spinal nerve foramina and the high chromosomal number are secondary features.

28. Salamandrids are descended from an ancestor shared with plethodontids and, in turn, gave rise to sirenids. Evidence for this comes

from spinal nerve patterns, chromosomal numbers (sirenids being tetraploid), trunk musculature, vertebral structure, and the middle ear.

29. Sirenids and salamandrids are included in a superfamily Salamandroidea.

30. Two subfamilies are recognized within the Salamandridae: the Salamandrinae for the more primitive *Salamandra* and *Chioglossa* and the derived Pleurodelinae for the newts. The latter is further subdivided into two tribes: the more primitive Pleurodelini for *Pleurodeles*, *Tylototriton*, and *Salamandrina* and the derived Triturini for the remainder of the newts. Within the Triturini are recognized the following generic groups: the *Notophthalmus* group (*Notophthalmus* and *Taricha*), the *Cynops* group (*Cynops*, *Paramesotriton*, *Hypselotriton*, and *Pachytriton*), the *Triturus* group (*Triturus* and *Neureergus*), and the *Euproctus* group (only *Euproctus*).

31. The frontosquamosal arch and its associated cranial structures are almost certainly derived within the Salamandridae, although they are primitive within the Pleurodelinae, some of which have secondarily reduced the arch.

32. Salamandrines are primitive with respect to trunk musculature, cranial anatomy, and courtship behavior.

33. The Pleurodelini are primitive with respect to courtship, the structure of the *rectus abdominus* in *Tylototriton* and *Salamandrina*, and in laying eggs in water, but derived with respect to salamandrines in cranial structure, vertebral structure, structure of the ribs, and in the trunk musculature, notably as regards the *subvertebralis*.

34. The Caudata are divided into two suborders: the primitive anterior basapophyseal, and amphicoelous Archaeocaudata (crypto-branchoids and ambystomatoids), and the derived, posterior basapophyseal/opisthocoelous Neocaudata (proteoids, plethodontoids, and salamandroids).

35. A tentative biogeographic reconstruction is proposed:

- i) Ambystomatids originated in and have probably never left North America. They find their ancestry in hynobiid or pro-hynobiid stock that entered North America well before the start of the Tertiary.
- ii) Scapherpetontids and amphiumids originated from primitive ambystomatid ancestors that are represented today by dicamptodontines. They may have originated on the shores of the Cretaceous midcontinental sea, where they are represented by Cretaceous and early Tertiary fossils.
- iii) Neocaudates originated in North America from ambystomatid or ambystomatid-like ancestry. None of the living families is closely representative of the early neocaudate group.

- iv) Proteoids probably originated in North America from this early Neocaudate group, but with subsequent early dispersal into Europe (*Palaeoproteus*, *Proteus*, and *Mioproteus*).
- v) The place of origin of salamandrids is uncertain. The oldest fossils and present centre of diversity are in Europe. If this reflects the true centre of origin, dispersal subsequently took place into Asia and North America.
- vi) Sirenids probably arose from salamandrids in North America in the later part of the Cretaceous, perhaps along the shores of the interior seaway. The deltaic lowlands of this sea also seem to have seen the origin of amphiumids, scapherpetontids, batrachosauroidids, and (perhaps) proteids.
- vii) The paedogenic North American salamanders (sirenids, amphiumids, and proteids) then dispersed eastward as the midcontinental sea retreated with the start of the Tertiary.

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TABLES

Table 1. Proposed classification of the family Ambystomatidae.

Family Ambystomatidae Hallowell 1857

Subfamily Dicamptodontinae Tihen 1958

Content: *Dicamptodon**, *Rhyacotriton**, ?*Ambystomichnus*.

Subfamily Ambystomatinae Hallowell 1857

Genus *Ambystoma* Tschudi 1838*A. macrodactylum* species groupContent: *A. macrodactylum**, *A. gracile**, ?*A. tihenii**.*A. maculatum* species groupContent: *A. maculatum**, *A. jeffersonianum**, *A. laterale*,
A. tremblayi, *A. platineum*.*A. opacum* species groupContent: *A. opacum**, *A. talpoideum**.*A. cingulatum* species groupContent: subgenus *Linguaelapsus* of Tihen (1958);
A. cingulatum available.*A. tigrinum* species groupContent: *A. mexicanum* species group, *A. tigrinum* species
group, and subgenus *Bathysiredon* of Tihen (1958),
A. tigrinum available.Genus *Rhyacosiredon* Dunn 1928

Content: as Tihen (1958).

*Available for study.

Table 2. Proposed classification of the family Plethodontidae.

Family Plethodontidae Gray 1850

Subfamily Plethodontinae Boulenger 1882

Tribe Plethodontini Wake 1966

Content: *Plethodon**, *Ensatina**, *Aneides**, *Hemidactylium**,
*Batrachoseps**.

Tribe Bolitoglossini Wake 1966

Content: *Bolitoglossa**, *Hydromantes**, *Lineatriton*,
Thorius, *Pseudoeurycea**, *Chiropterotriton**,
Oedipina, *Parvimolge*.

Subfamily Desmognathinae Boulenger 1882

Tribe Euryciini Wake & Lombard 1973

Content: *Eurycea**, *Gyrinophilus**, *Pseudotriton**,
*Stereochilus**, *Haideotriton*, *Typhlotriton**,
Typhlomolge.

Tribe Desmognathini nov.

Content: *Desmognathus**, *Leurognathus**, *Phaeognathus*.

*Available for study.

Table 3. Proposed classification of the family Salamandridae,
fossil taxa not included.

Family Salamandridae Gray 1825

Subfamily Salamandrinae Tschudi 1838

Content: *Salamandra**, *Chioglossa*.

Subfamily Pleurodelinae nov.

Tribe Pleurodelini Bonaparte 1838

Content: *Pleurodeles**, *Tylototriton**, *Salamandrina**.

Tribe Triturini nov.

Notophthalmus group

Content: *Notophthalmus**, *Taricha**.

Cynops group

Content: *Cynops**, *Paramesotriton**, *Hypselotriton*
Pachytriton.

Triturus group

Content: *Triturus**, *Neurergus*.

Euproctus group

Content: *Euproctus**.

*Available for study.

Table 4. Proposed classification of the order Caudata.

Order Caudata Oppel 1811

Suborder Archaeocaudata nov.

Superfamily Cryptobranchoidea Fitzinger 1826

Family Hynobiidae Cope 1860

Family Cryptobranchidae Cope 1889

Superfamily Ambystomatoidea Noble 1931

Family Scapherpetontidae Auffenberg & Goin 1959

Family Amphiumidae Gray 1825

Family Ambystomatidae Hallowell 1857

Subfamily Dicamptodontinae Tihen 1958

Subfamily Ambystomatinae Hallowell 1957

?Archaeocaudata *incertae sedis*

Family Prosirenidae Estes 1969

Suborder Neocaudata nov.

Superfamily Proteoidea Muller 1831

Family Batrachosauroididae Auffenberg 1958

Family Proteidae Hogg 1838

Superfamily Plethodontoidea Smith & Taylor 1948

Family Plethodontidae Gray 1850

Subfamily Plethodontinae Boulenger 1882

Tribe Plethodontini Wake 1966

Tribe Bolitoglossini Wake 1966

Subfamily Desmognathinae Boulenger 1882

Tribe Euryciini Wake & Lombard 1973

Tribe Desmognathini nov.

Superfamily Salamandroidea Fitzinger 1826

Family Salamandridae Gray 1825

Subfamily Salamandrinae Tschudi 1838

Subfamily Pleurodelinae nov.

Tribe Pleurodelini Bonaparte 1838

Tribe Triturini nov.

Family Sirenidae Gray 1825

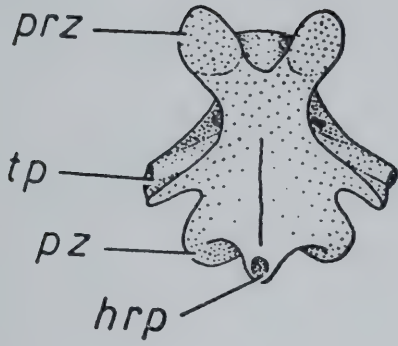
FIGURES

Figure 1. Vertebrae of selected species of salamanders, showing features and terminology discussed in the text:

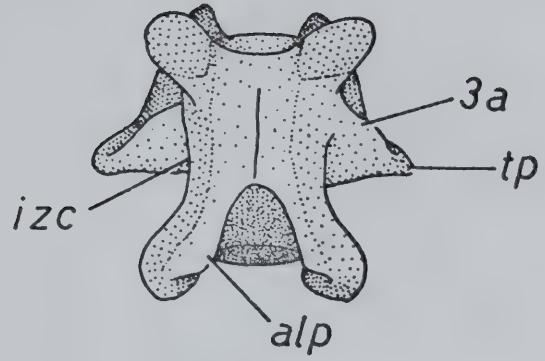
(A) *Necturus maculosus*, dorsal view; (B) *Desmognathus fuscus*, lateral view; (C) *Amphiuma tridactylum*, ventral view; (D) *Siren lacertina*, dorsal view; (E) same, lateralview; (F) *Amphiuma tridactylum*, posterior view.

Abbreviations explained on pp. 4-7.

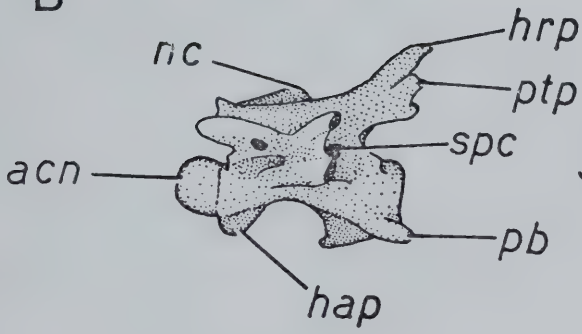
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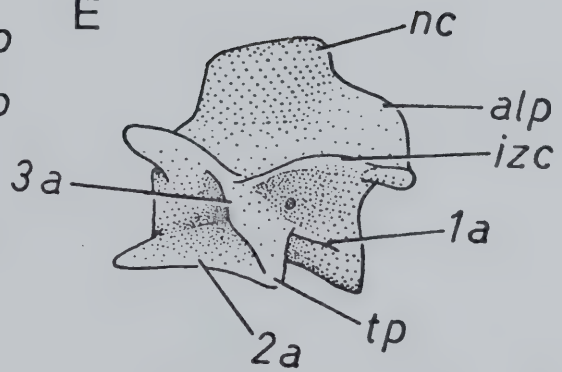
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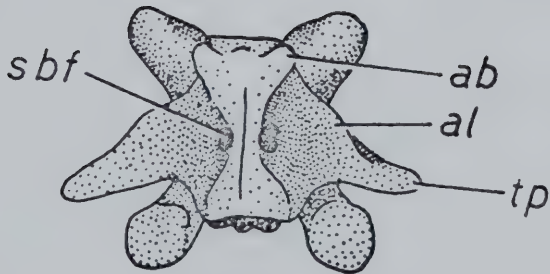
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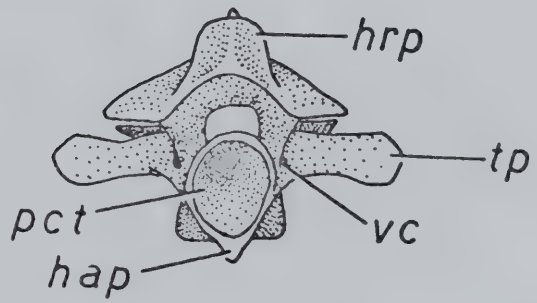
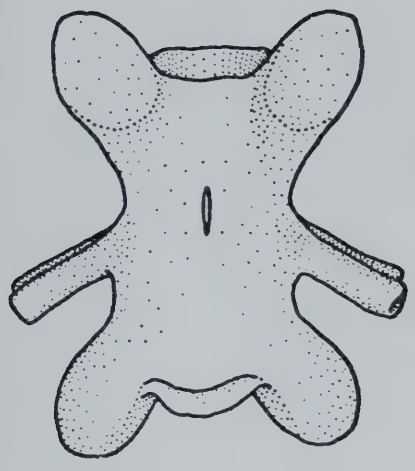


Figure 2. Midtrunk vertebrae of hynobiid salamanders in dorsal, ventral, and lateral views: (A) *Pachypalaminus boulengeri*, T8; (B) *Onychodactylus japonicus*, T9; scale represents one millimeter.

A



B

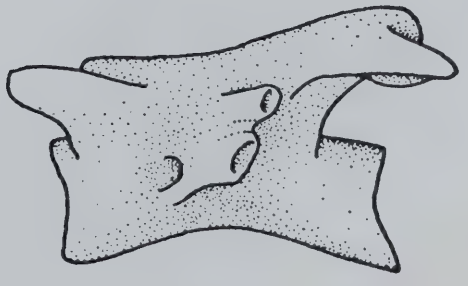
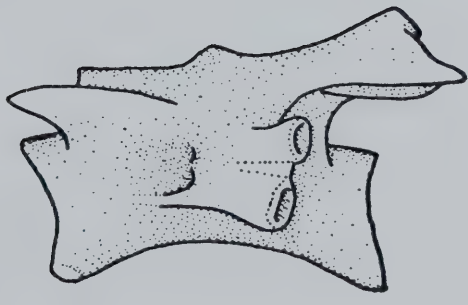
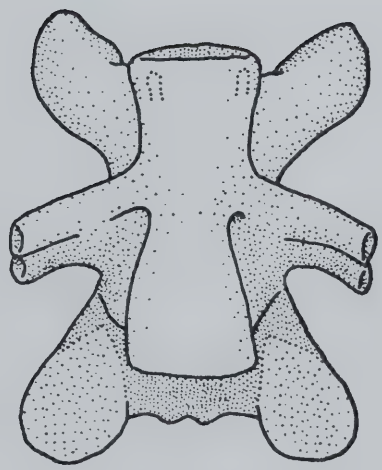
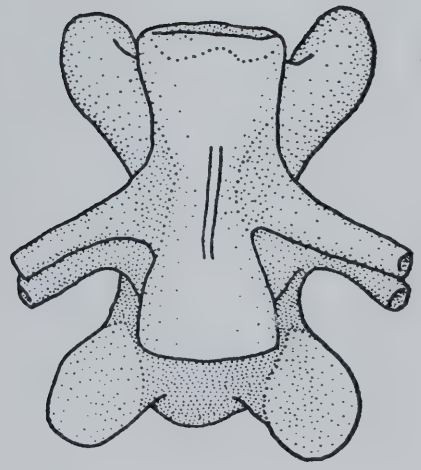
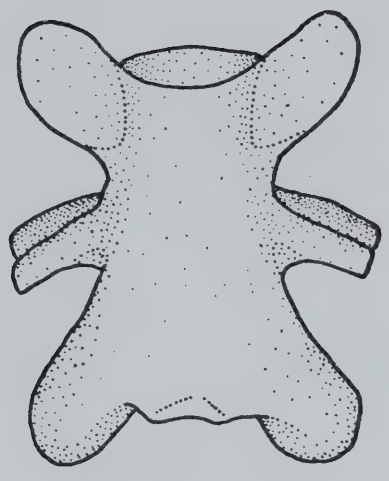


Figure 3. Midtrunk vertebrae of cryptobranchoid salamanders in dorsal, ventral, and lateral views: (A) *Hynobius naevius*, T8; (B) *Cryptobranchus alleganiensis*, T9; scale represents one millimeter.

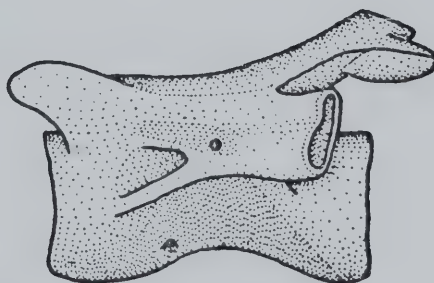
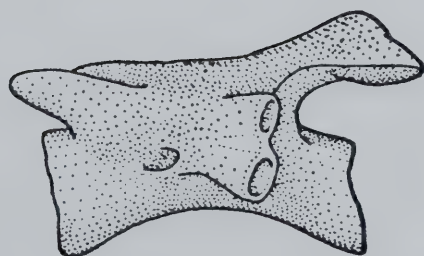
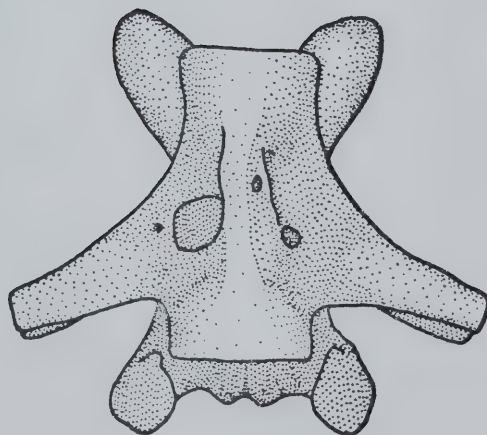
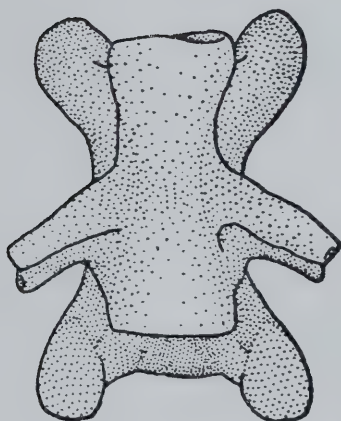
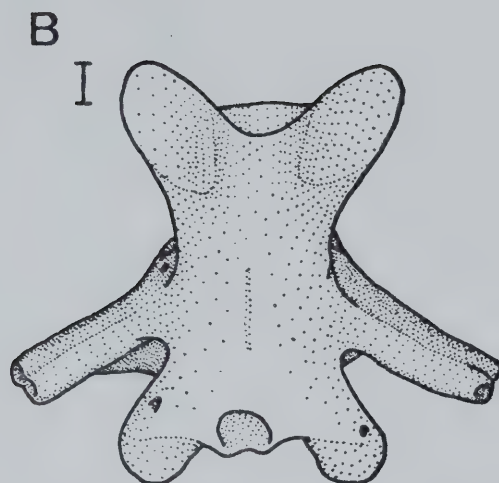
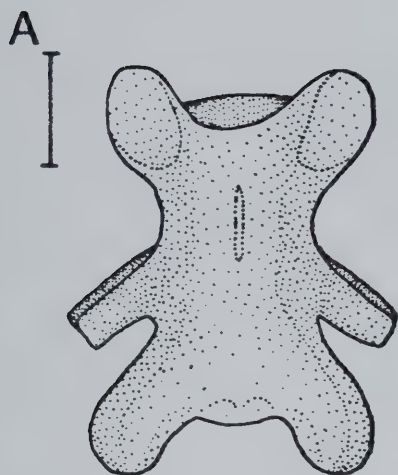


Figure 4. Midtrunk vertebra of *Amphiuma tridactylum* in dorsal, ventral, and lateral views; scale represents one millimeter.

I

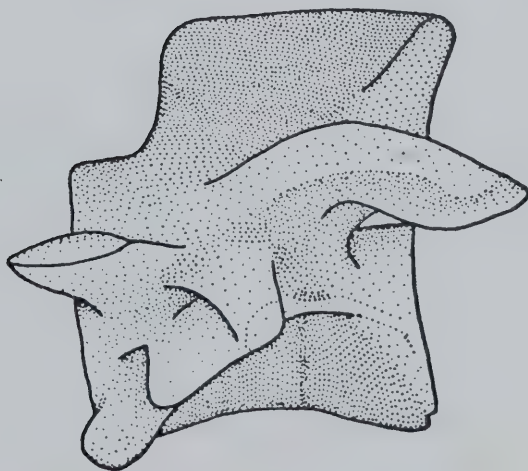
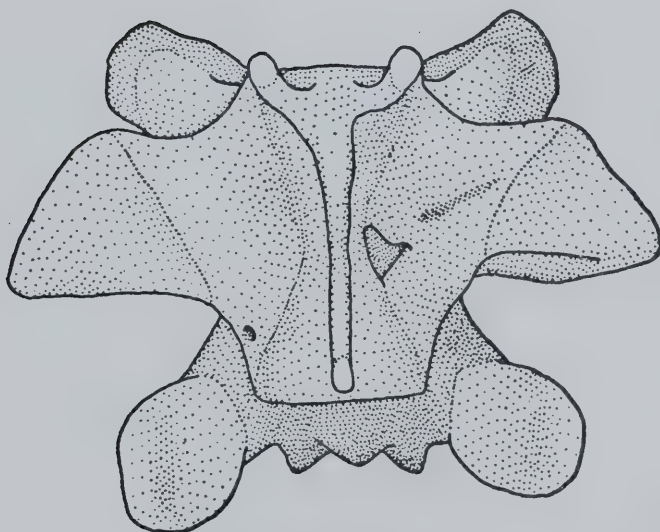
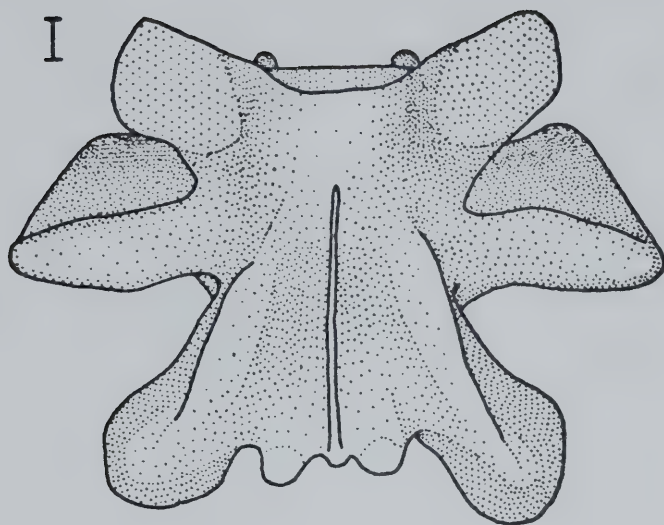


Figure 5. Trunk vertebra of *Ambystoma tihenii* (SMNH 1431) in dorsal, ventral, and lateral views; from the Oligocene of southern Saskatchewan; scale represents one millimeter.

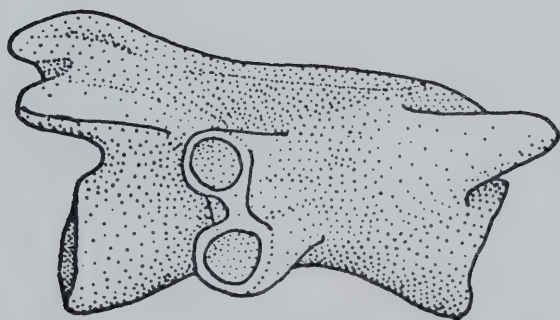
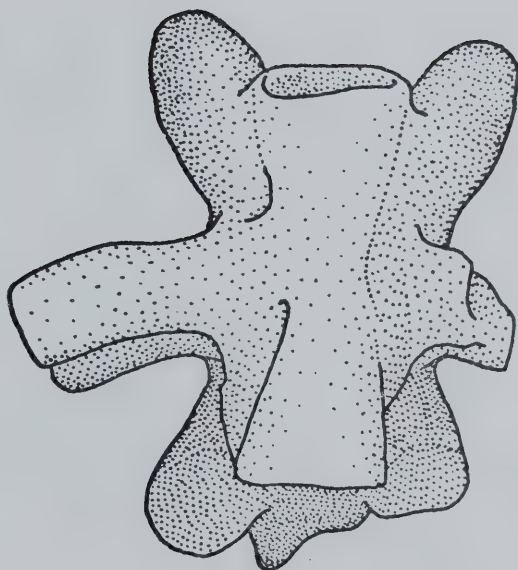
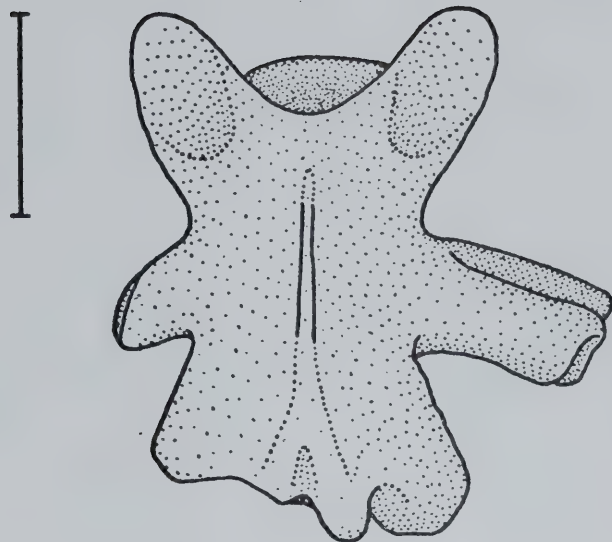


Figure 6. Midtrunk vertebrae of ambystomatid salamanders in dorsal, ventral, and lateral views; (A) *Ambystoma maculatum*, T8; (B) *Ambystoma jeffersonianum*, T8; scale represents one millimeter.

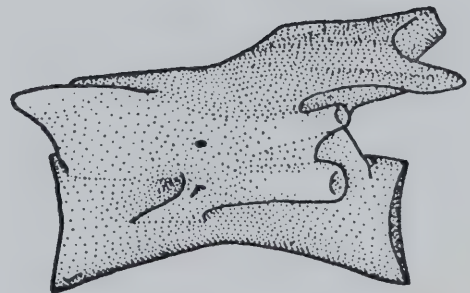
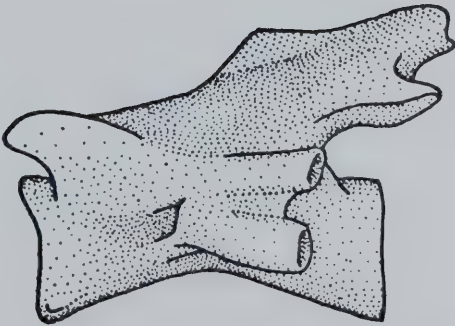
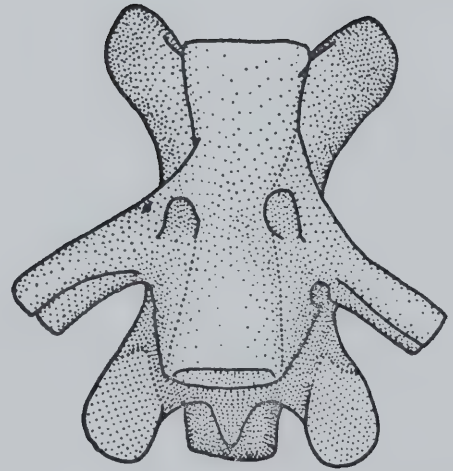
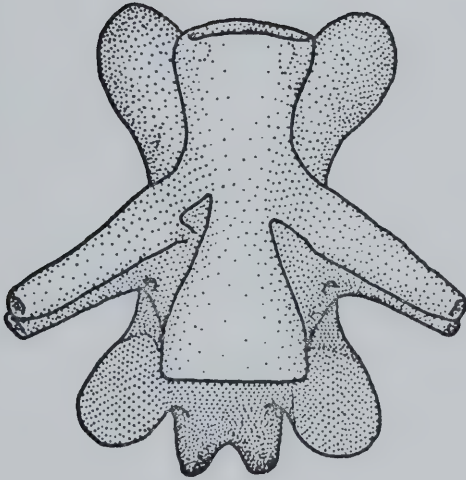
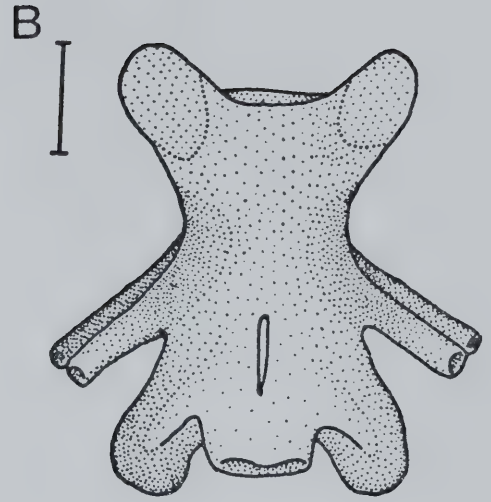
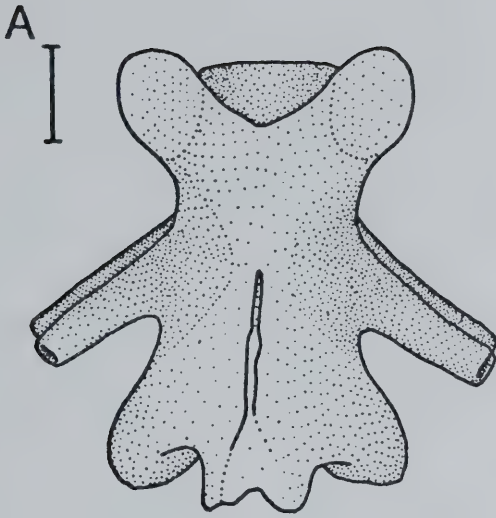
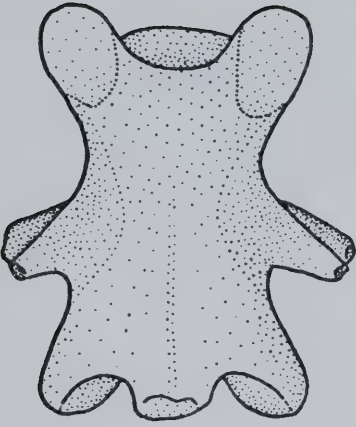


Figure 7. Midtrunk vertebrae of ambystomatid salamanders in dorsal, ventral, and lateral views: (A) *Ambystoma gracile*, T8; (B) *Ambystoma talpoidum*, T8; scale represents one millimeter.

A



B

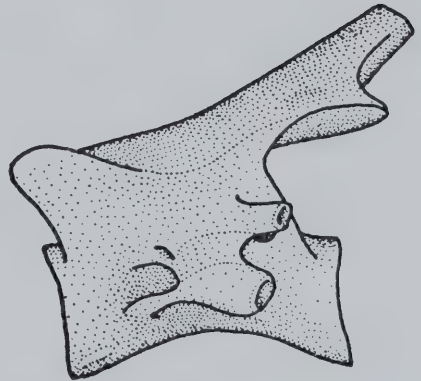
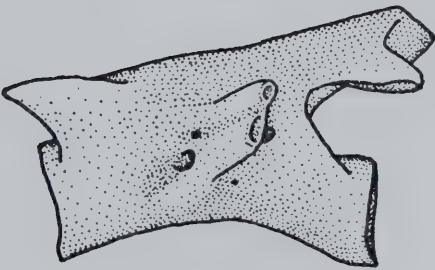
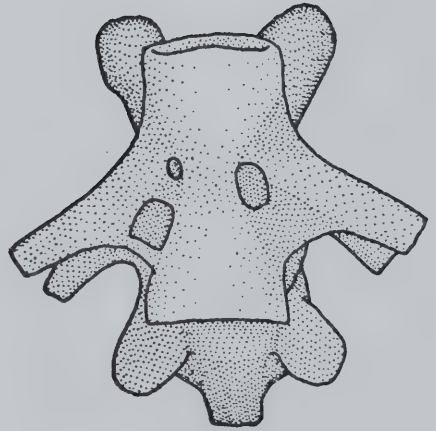
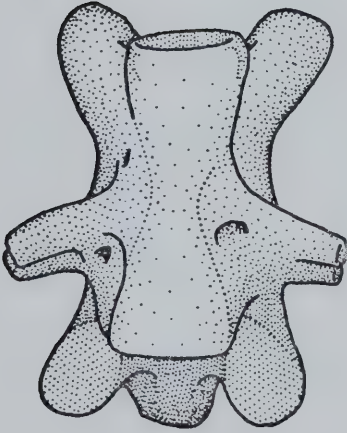
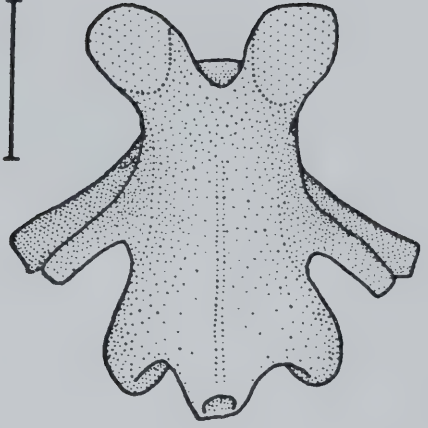


Figure 8. Atlas of young, postmetamorphic *Ambystoma tigrinum*
in anterior, posterior, dorsal, ventral, and lateral
views; scale represents one millimeter.

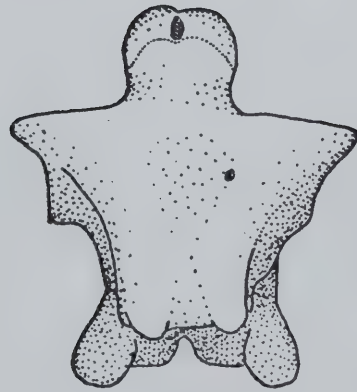
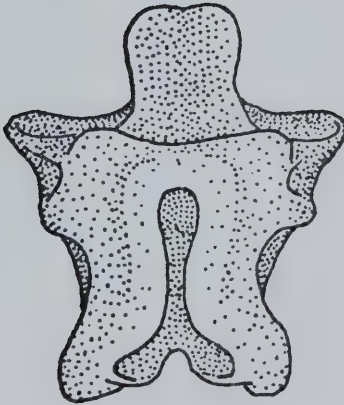
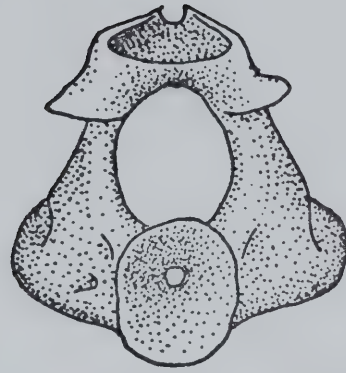
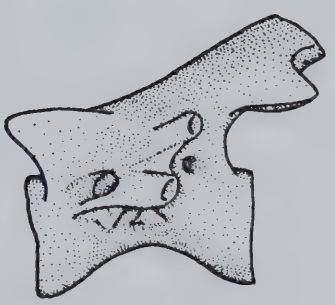
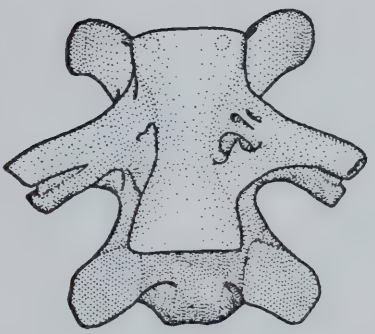
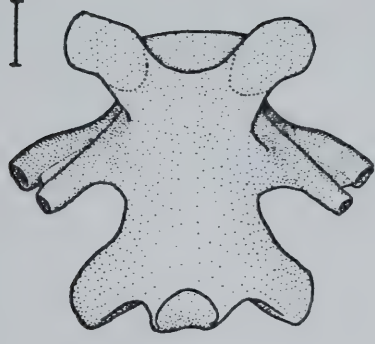
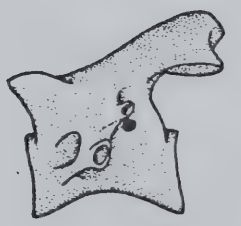
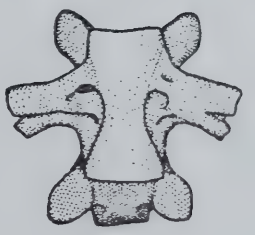


Figure 9. Midtrunk vertebrae of *Ambystoma tigrinum* in dorsal, ventral, and lateral views: (A) large metamorphosed *Ambystoma tigrinum diaboli*, T8; (B) small metamorphosed *Ambystoma tigrinum melanostictum*, T8; (C) neotenic individual of the same subspecies, T8; scale represents one millimeter.

A
|



B



C

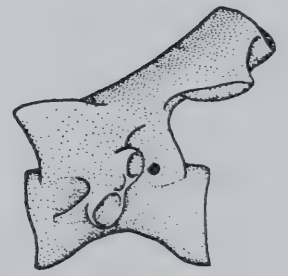
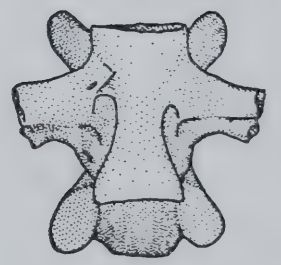
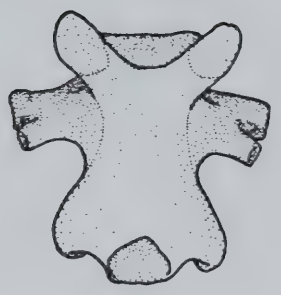


Figure 10. Atlas of *Necturus maculosus* in anterior, posterior, dorsal, ventral, and lateral views; scale represents two millimeters.

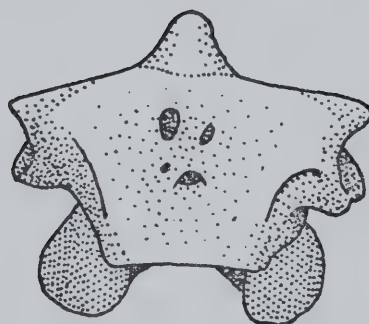
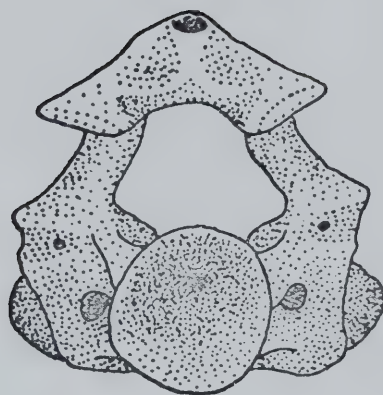
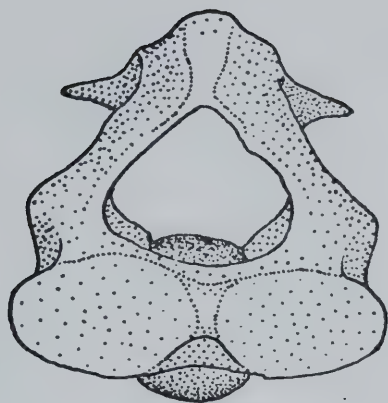


Figure 11. Atlas of *Siren lacertina* in anterior, posterior, dorsal, ventral, and lateral views; scale represents two millimeters.

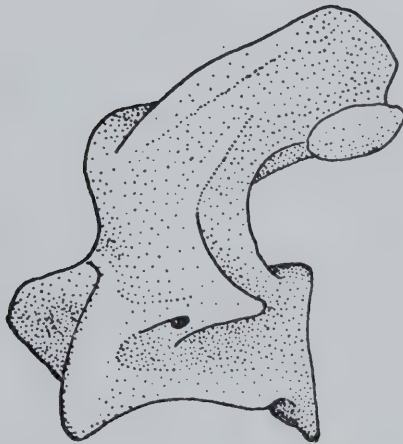
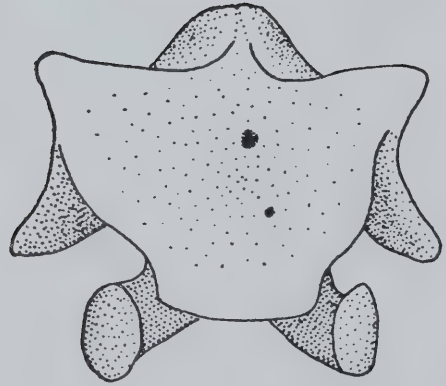
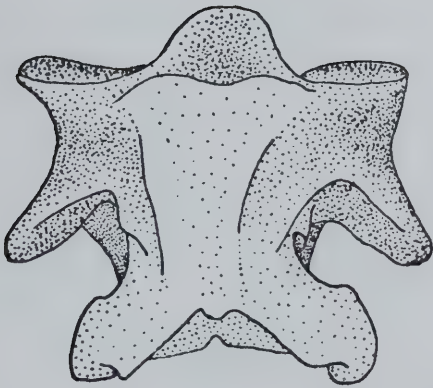
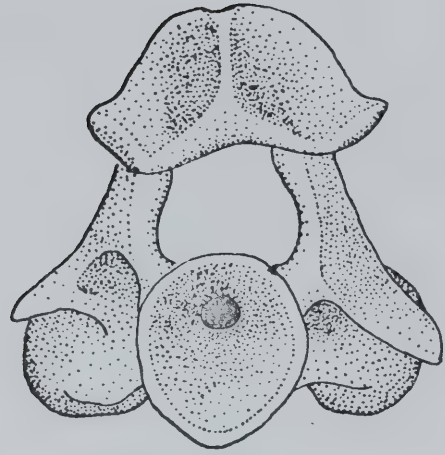
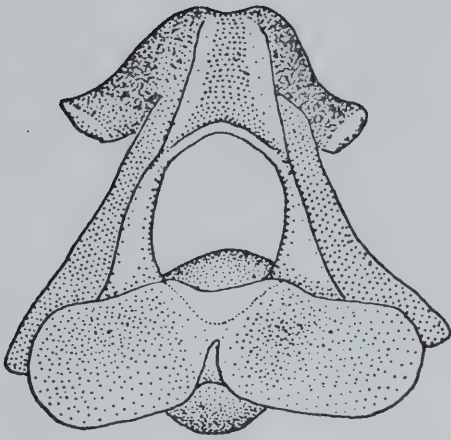
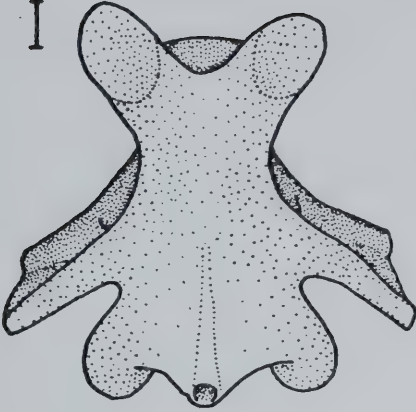


Figure 12. Midtrunk vertebrae in dorsal, ventral, and lateral views: (A) *Necturus maculosus*; (B) *Siren lacertina*; scale represents one millimeter.

A

I



B

I

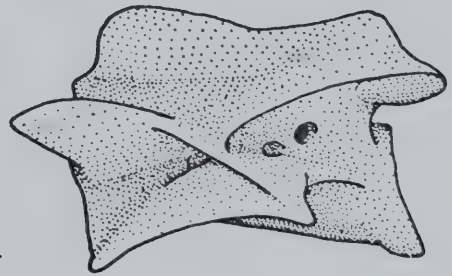
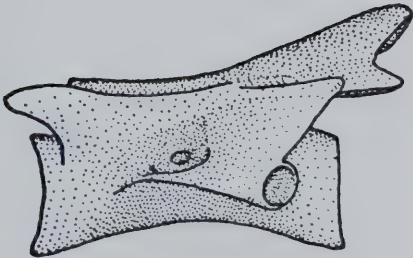
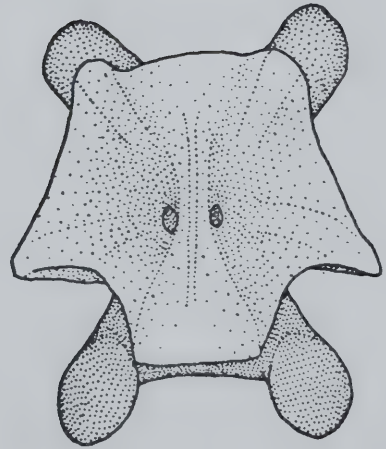
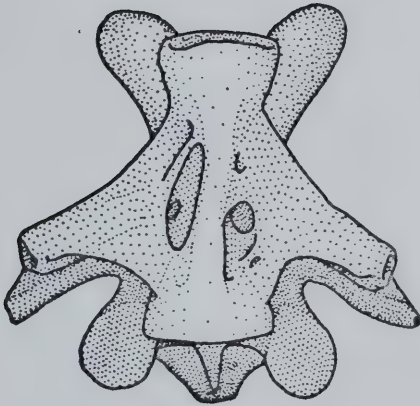
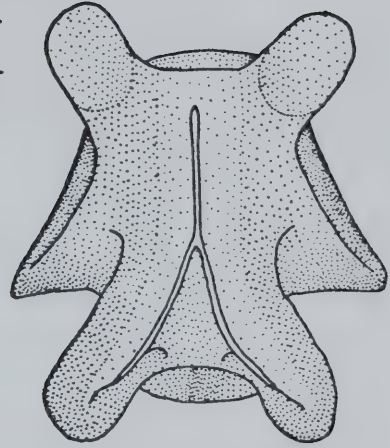
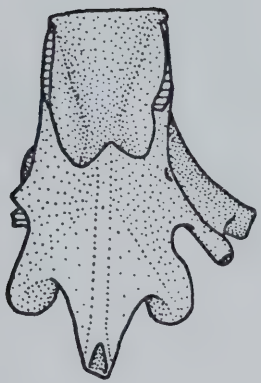


Figure 13. Trunk vertebrae of *Necturus* in dorsal, ventral, and lateral views: (A) UA 14310; (B) UA 14311; both from the Paleocene Ravenscrag Formation, Saskatchewan; scale represents one millimeter;

A
|



B

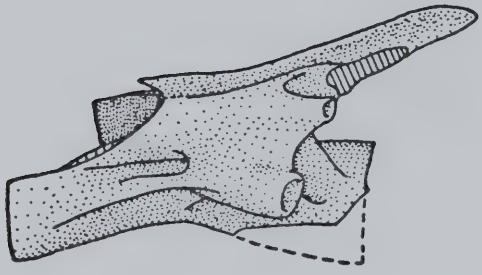
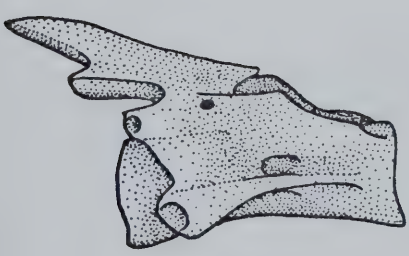
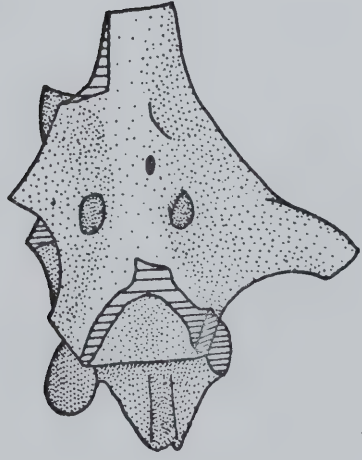
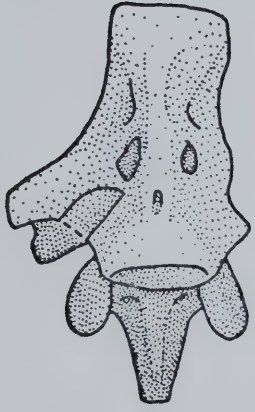
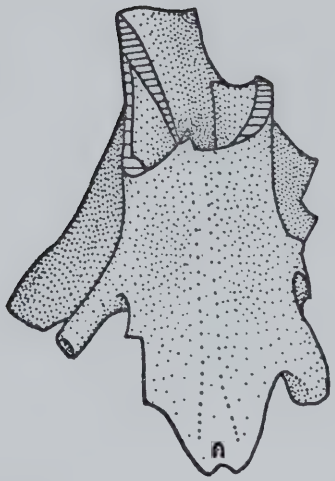


Figure 14. Midtrunk vertebrae of plethodontid salamanders in dorsal, ventral, and lateral views: (A) *Plethodon jordani*; (B) *Aneides lugubris*, T8; scale represents one millimeter.

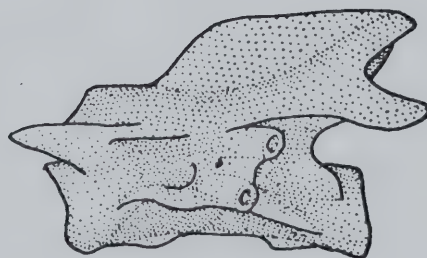
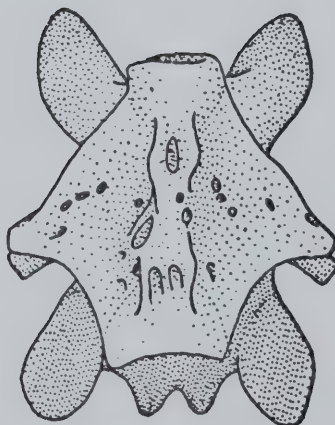
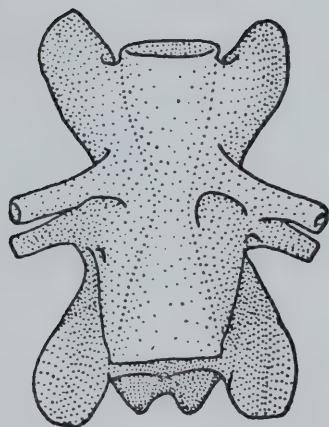
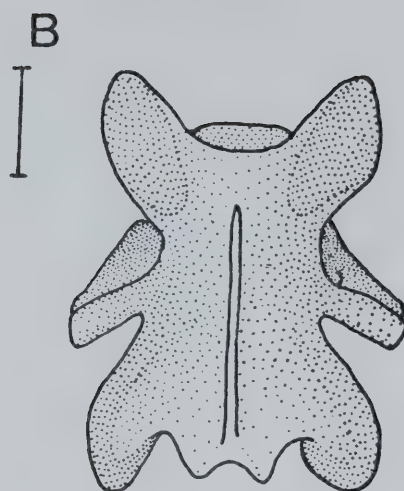
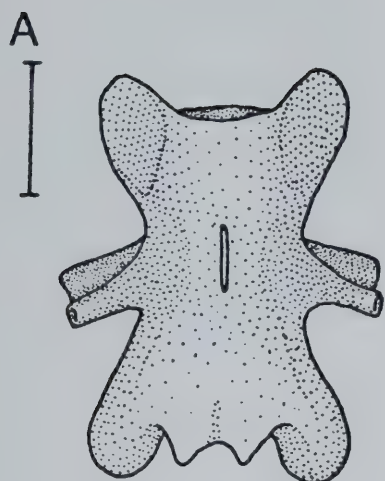


Figure 15. Atlas of *Desmognathus fuscus* in anterior, posterior, dorsal, ventral, and lateral views; scale represents two millimeters.

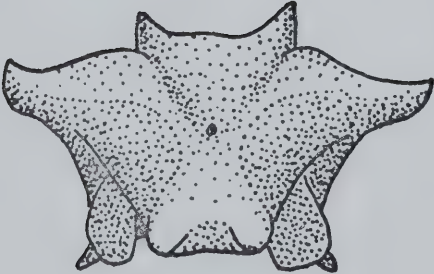
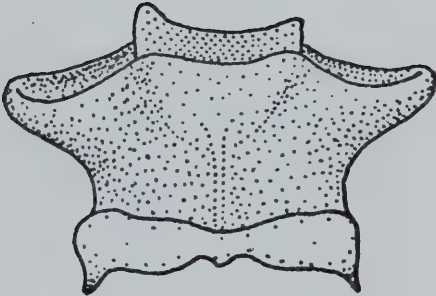
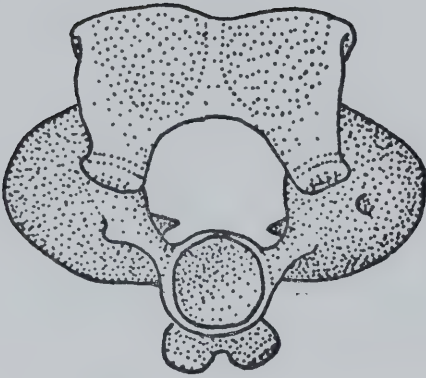
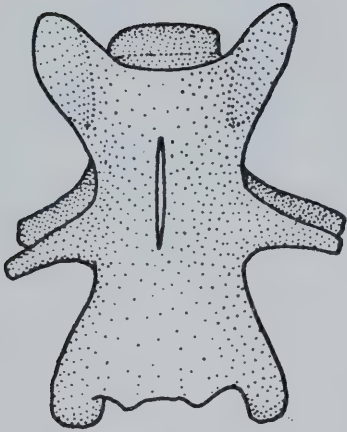


Figure 16. Midtrunk vertebrae of plethodontid salamanders in dorsal, ventral, and lateral views: (A) *Pseudotriton ruber*, T8: (B) *Desmognathus fuscus*; scale represents one millimeter.

A
|



B
|

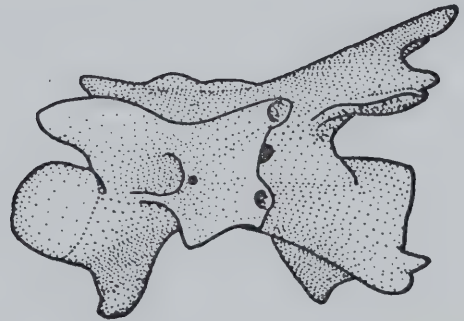
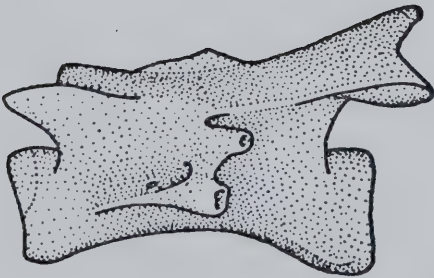
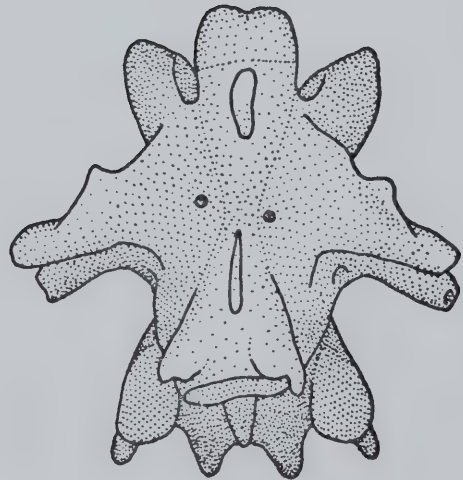
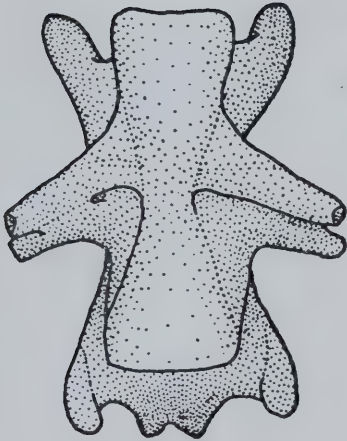
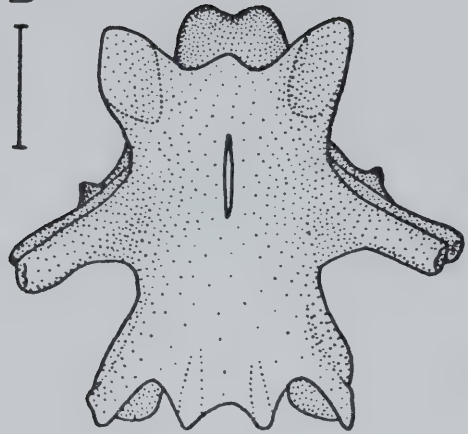


Figure 17. Atlas of *Salamandra salamandra* in anterior, posterior, dorsal, ventral, and lateral views; scale represents two millimeters.

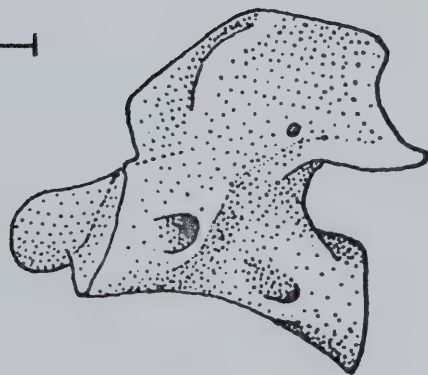
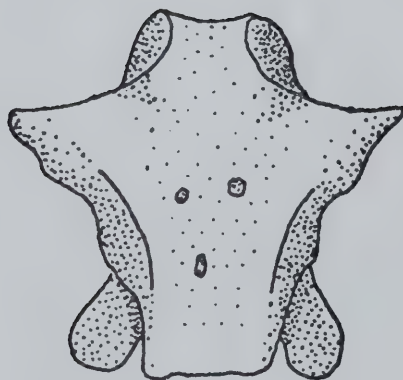
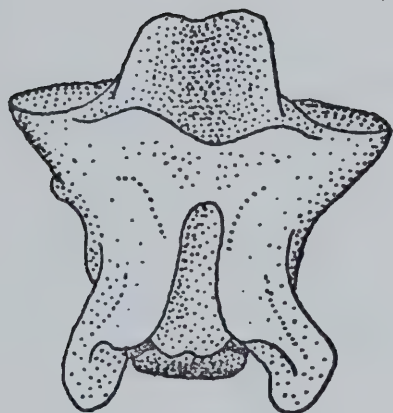
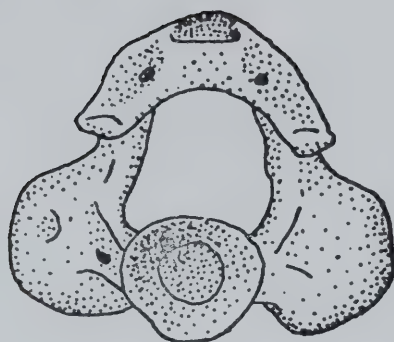
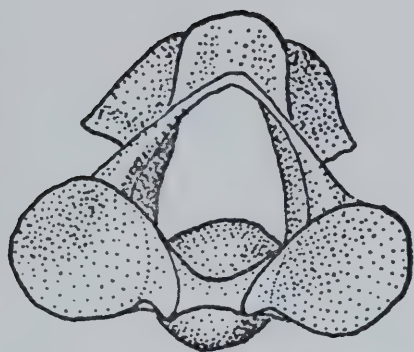
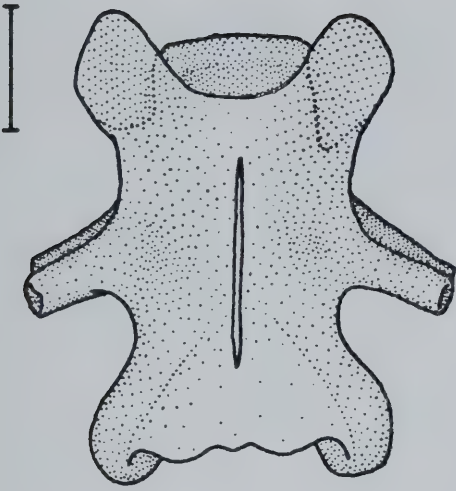


Figure 18. Midtrunk vertebrae of salamandrid salamanders in dorsal, ventral, and lateral views: (A) *Salamandra salamandra*; (B) *Pleurodeles waltli*, T8; scale represents one millimeter.

A



B

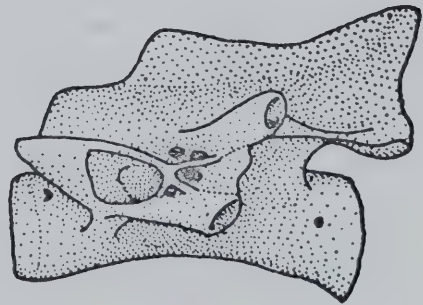
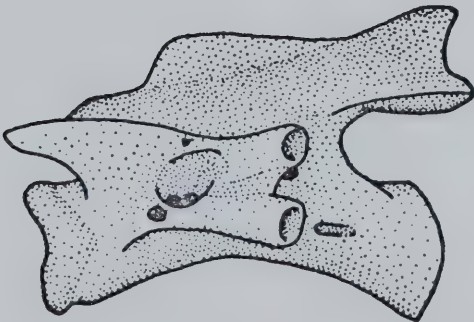
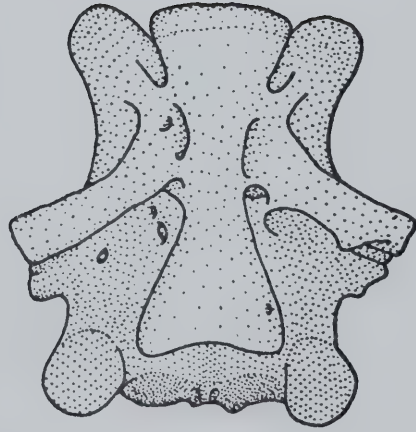
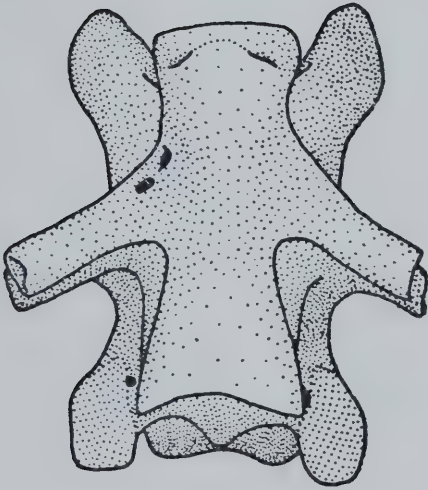
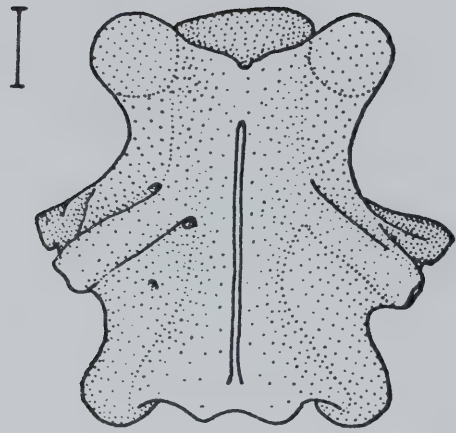
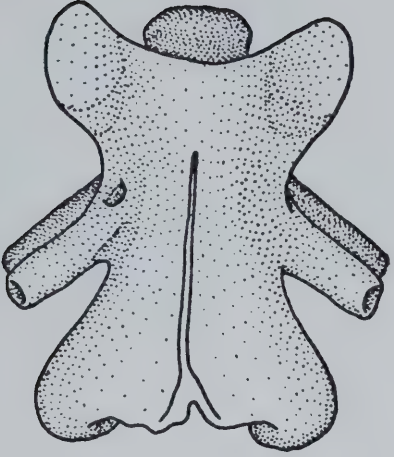


Figure 19. Midtrunk vertebrae of North American salamandrids in dorsal, ventral, and lateral views: (A) *Taricha* species, T7; (B) *Notophthalmus viridescens*, T7; scale represents one millimeter.

A



B

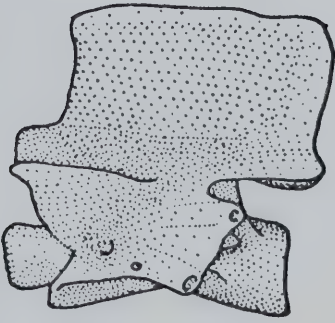
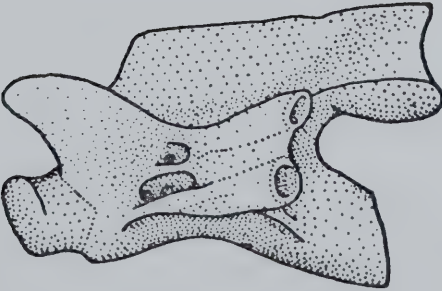
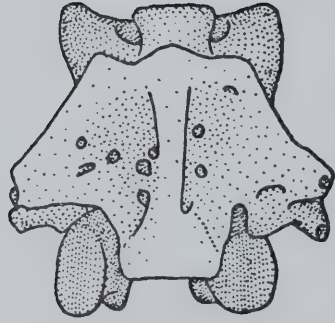
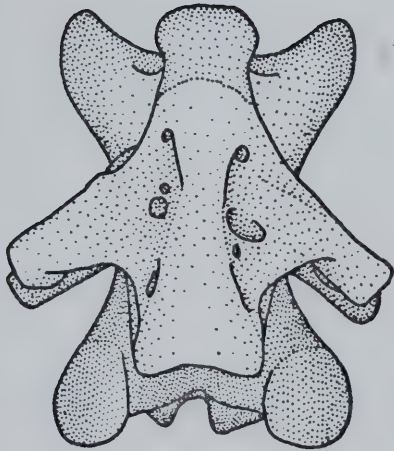
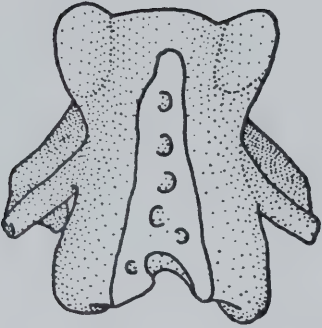


Figure 20. Atlas of *Triturus alpestris* in anterior, posterior, dorsal, ventral, and lateral views; scale represents one millimeter.

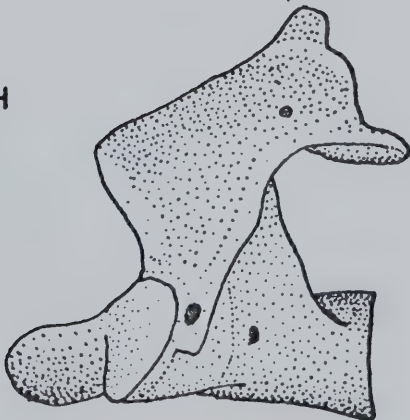
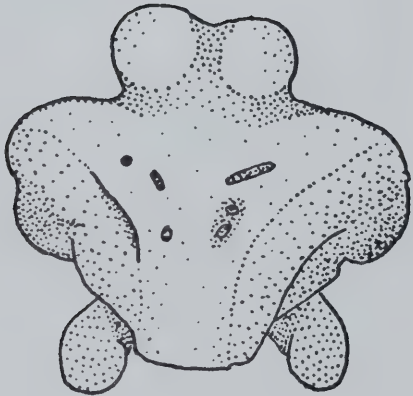
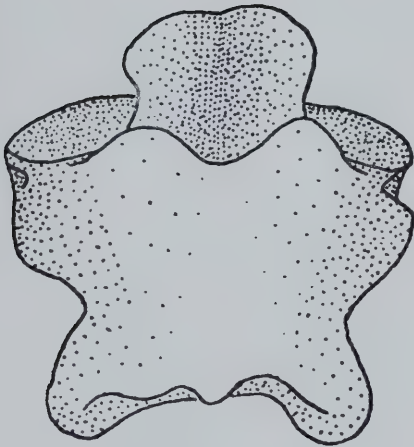
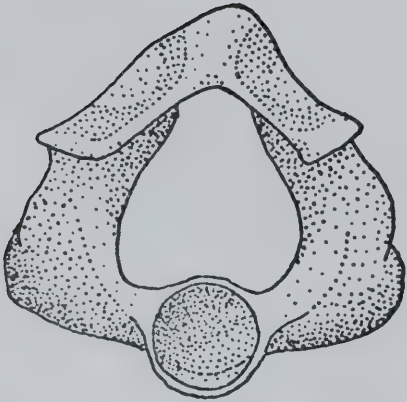
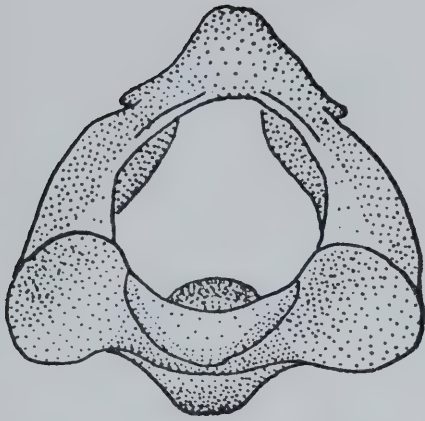
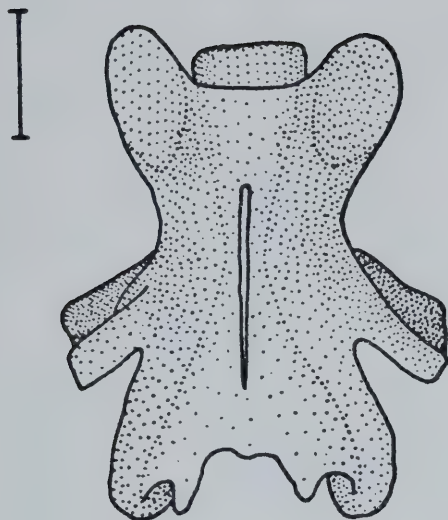


Figure 21. Midtrunk vertebrae of salamandrid salamanders in dorsal, ventral, and lateral views: (A) *Triturus cristatus*, T8; (B) *Triturus vulgaris*, T8; scale represents one millimeter.

A



B

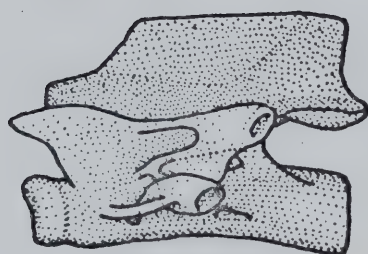
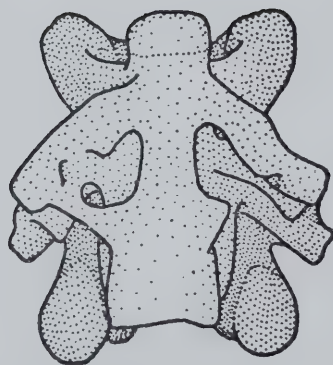
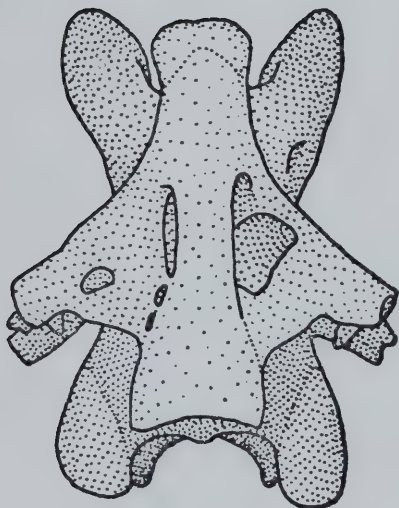
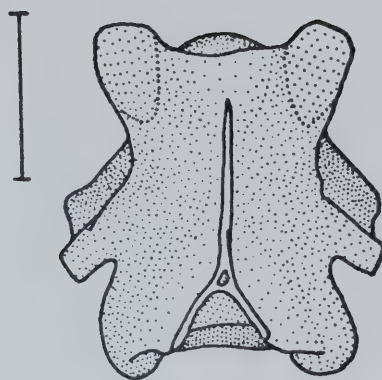


Figure 22. Dissection of *Hynobius retardatus* with lateral abdominal musculature spread laterally: (A) dorsal view; (B) ventral view; scale represents two millimeters; abbreviations given on pp. 4-7.

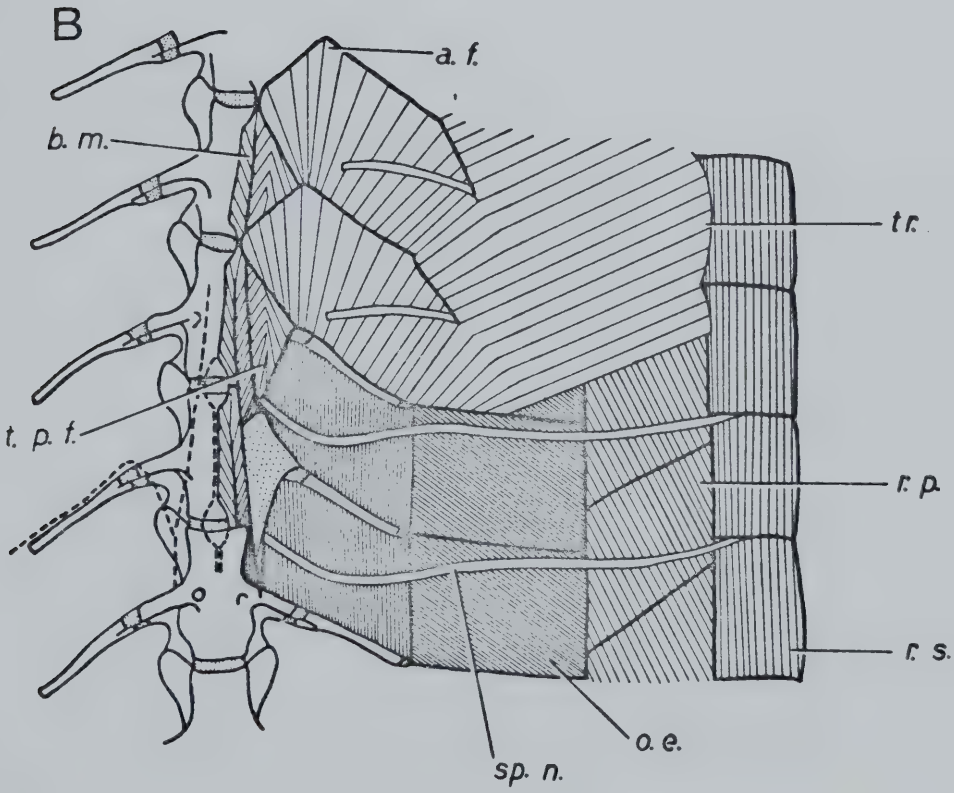
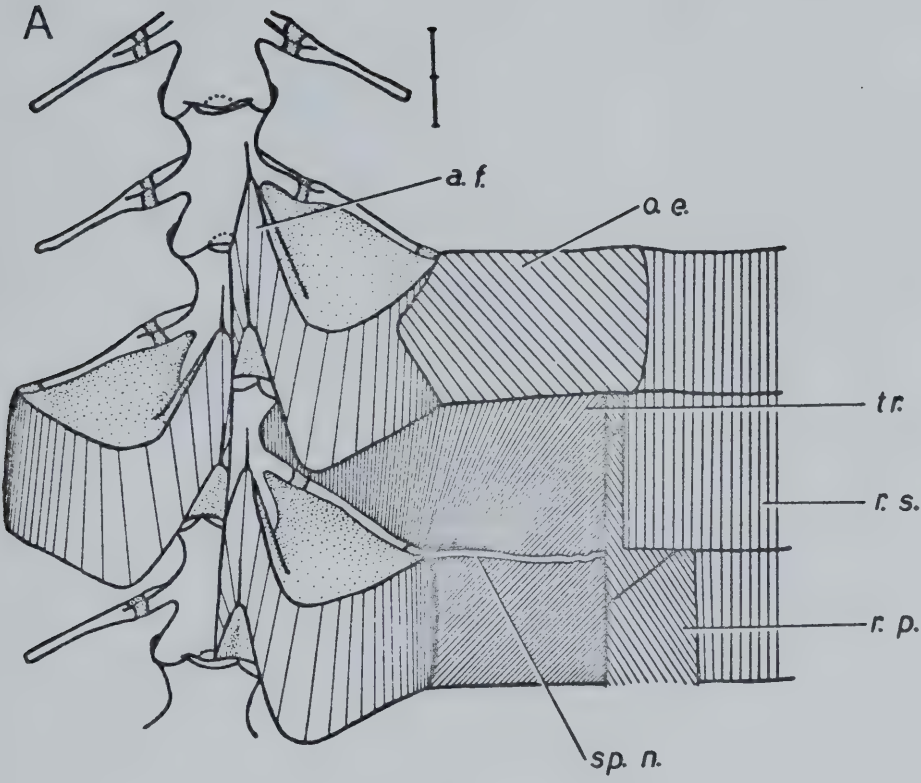


Figure 23. Dissection of *Hynobius naevius* with lateral abdominal musculature spread laterally: (A) dorsal view; (B) ventral view; scale represents two millimeters; abbreviations given on pp. 4-7.

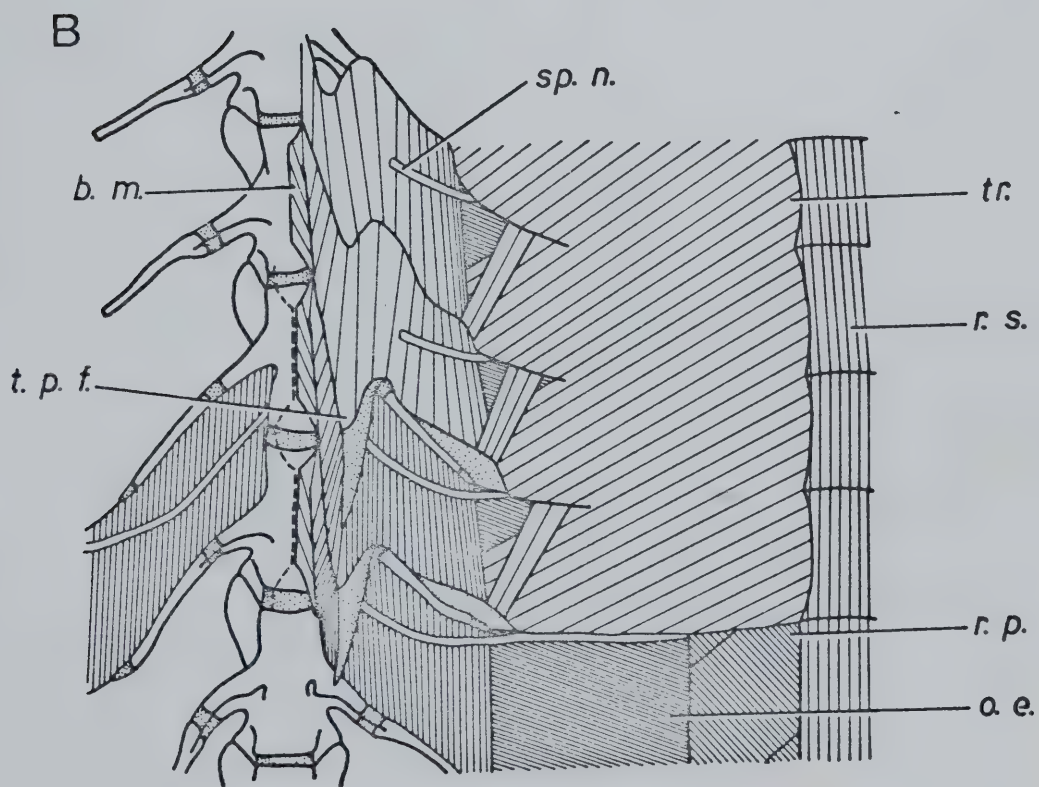
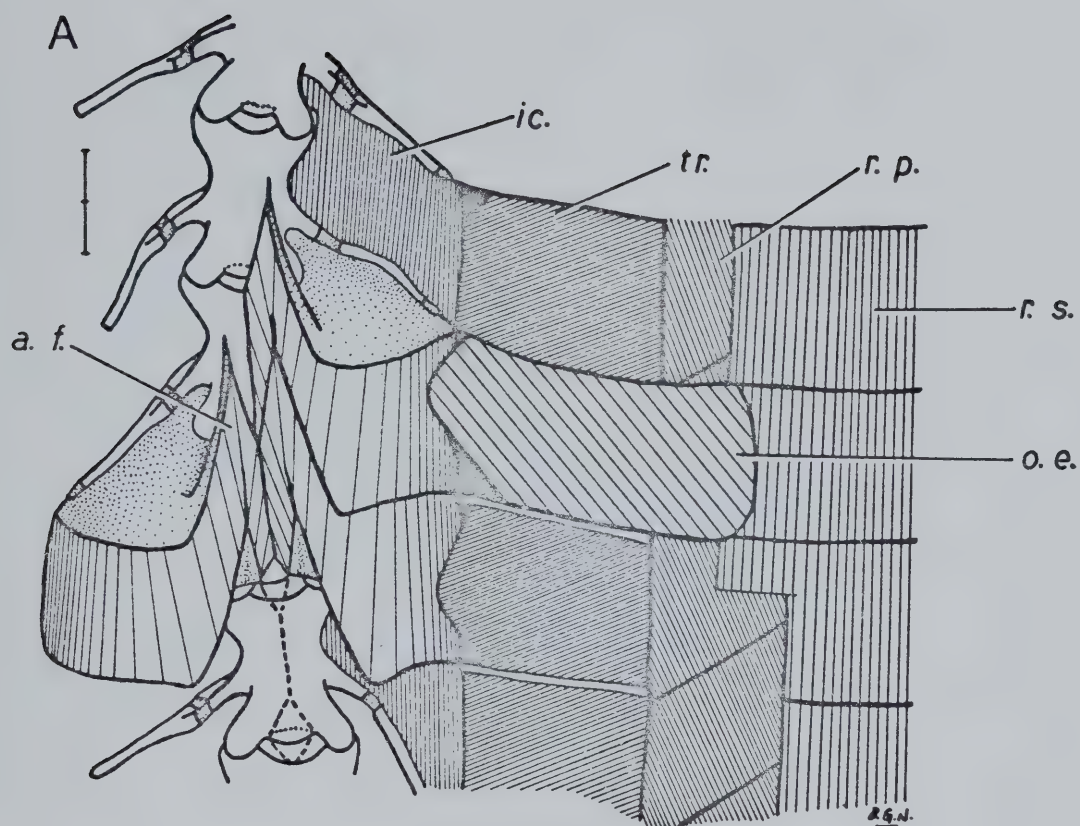


Figure 24. Dissection of *Pachypalaminus boulengeri* with lateral abdominal musculature spread laterally: (A) dorsal view; (B) ventral view; scale represents two millimeters; abbreviations given on pp. 4-7.

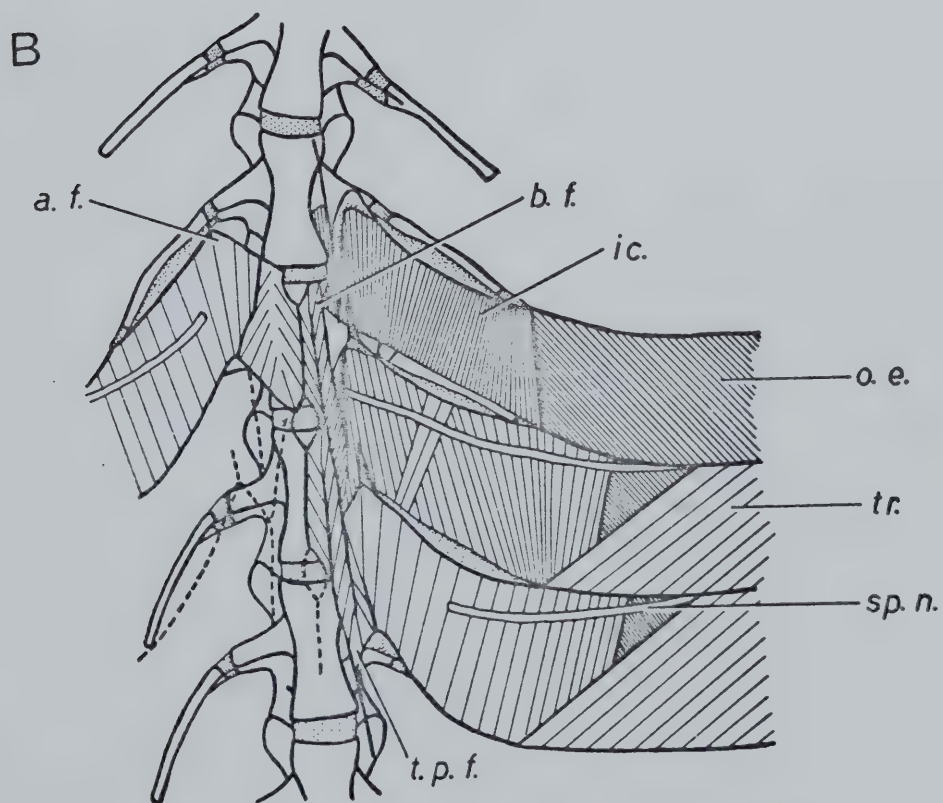
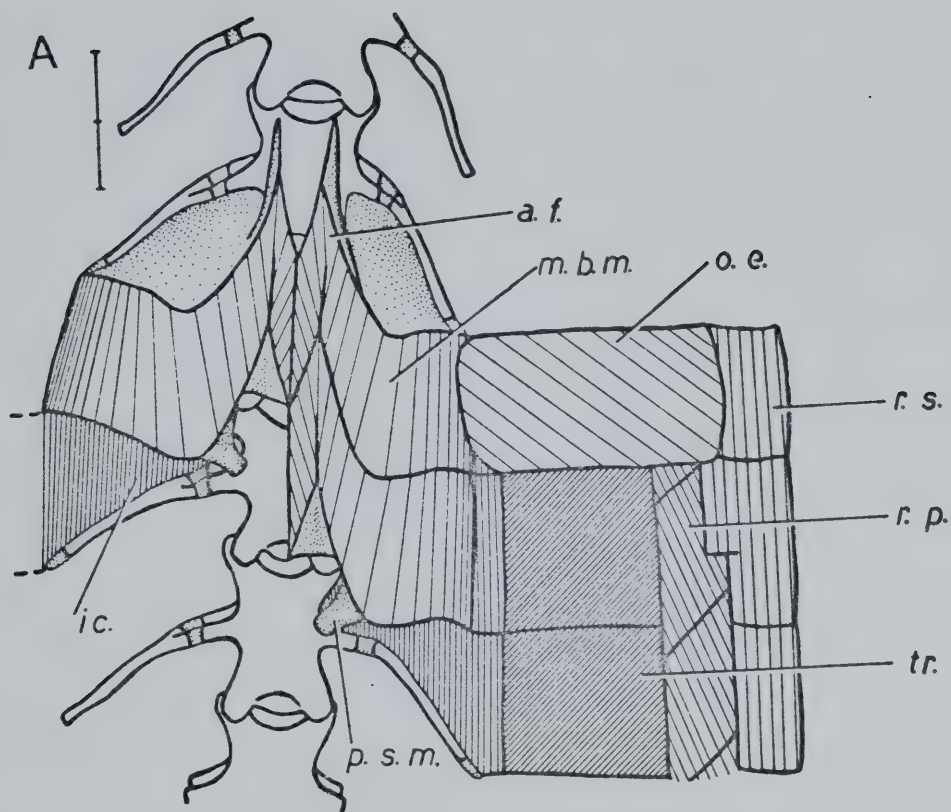


Figure 25. Dissection of *Onychodactylus japonicus* with lateral abdominal musculature spread laterally: (A) dorsal view; (B) ventral view; scale represents two millimeters; abbreviations given on pp. 4-7.

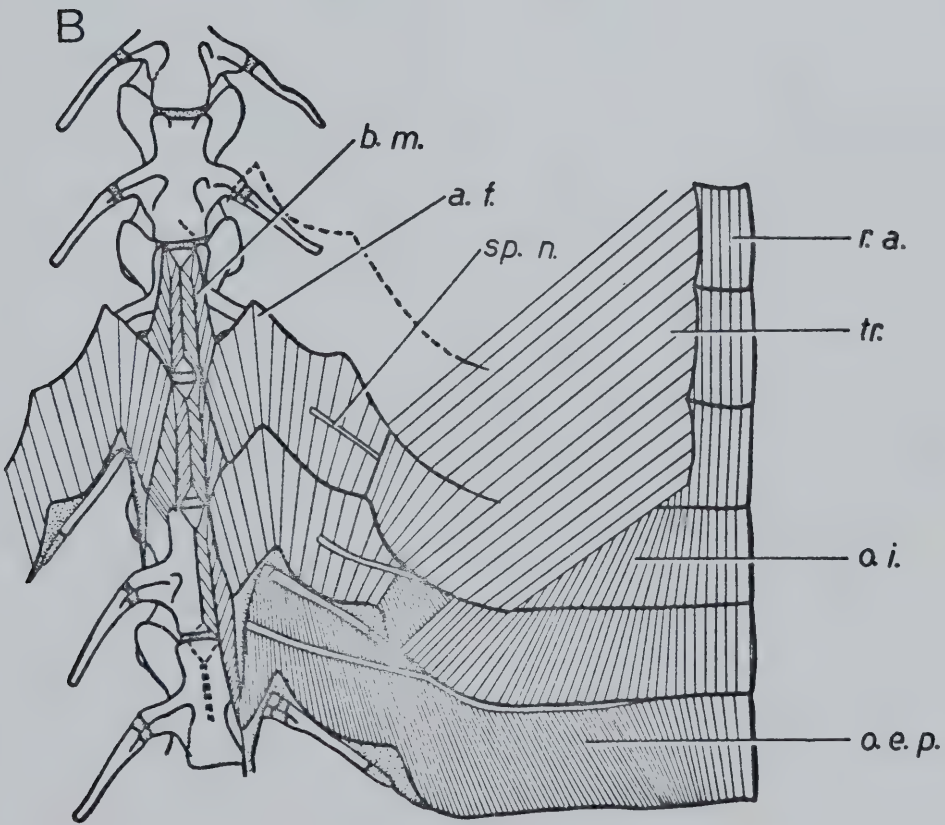
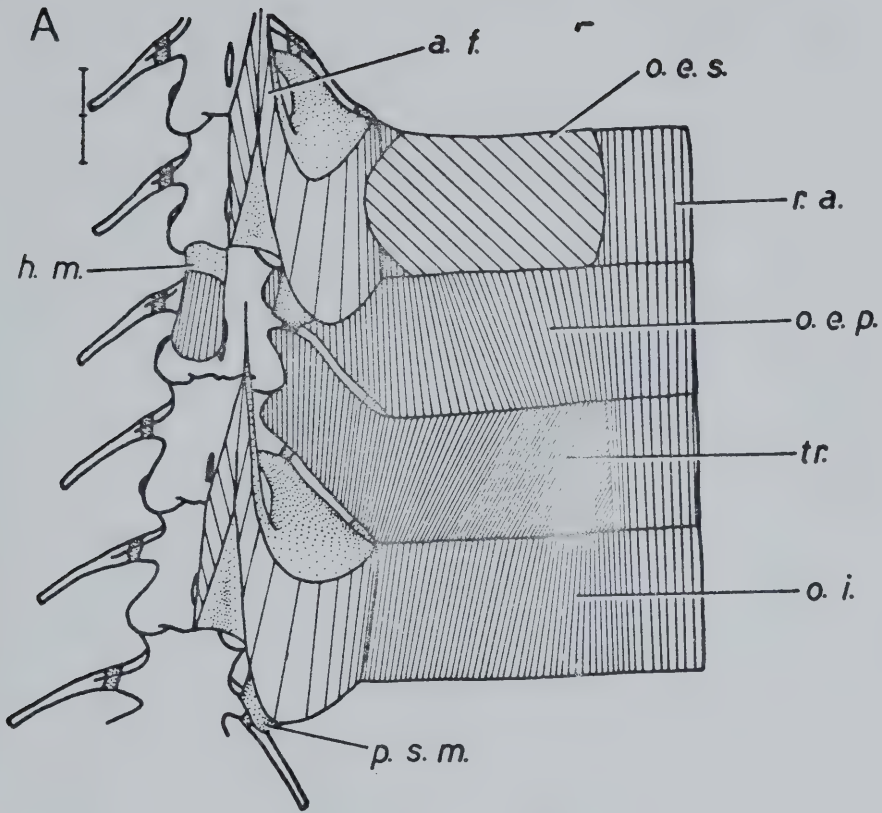


Figure 26. Cross-sections through the trunk musculature of
hynobiid and ambystomatid salamanders: (A) *Hynobius*;
(B) *Onychodactylus*; (C) *Ambystoma jeffersonianum*;
(D) *Ambystoma talpoides*; abbreviations given on
pp. 4-7.

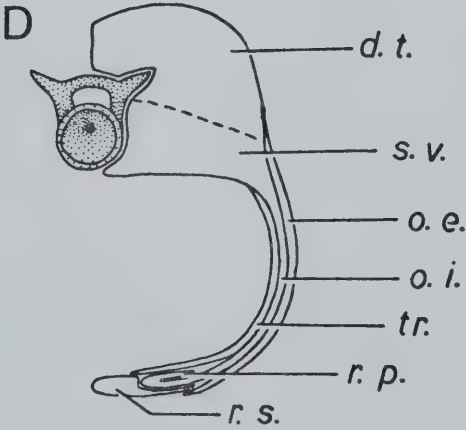
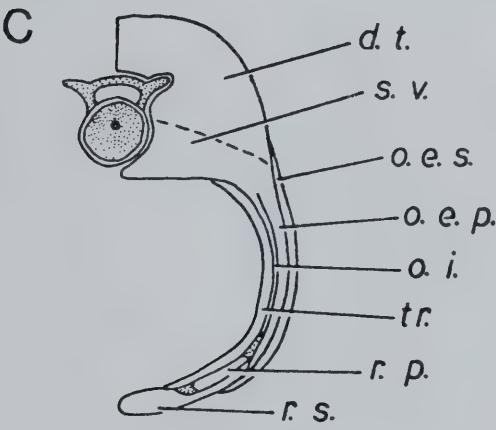
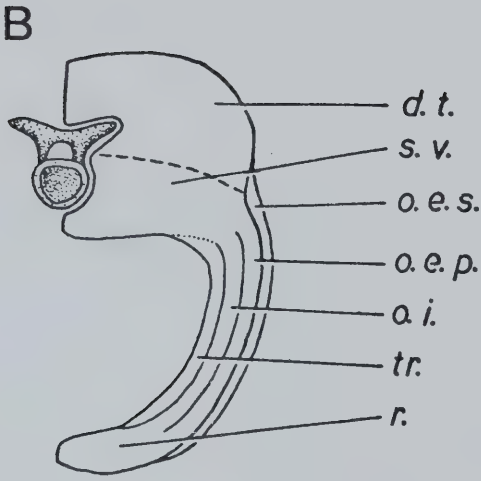
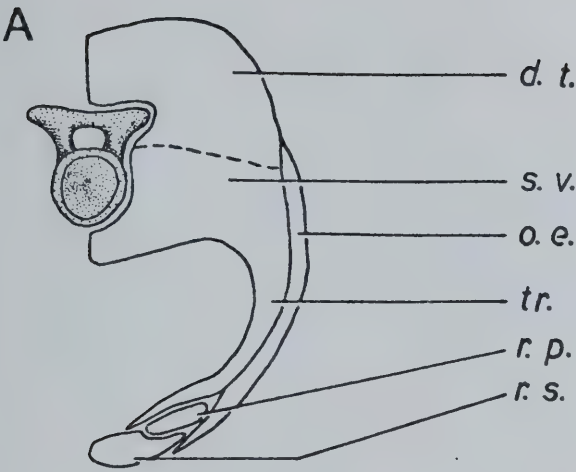


Figure 27. Dissection of *Cryptobranchus alleganiensis* with lateral abdominal musculature spread laterally: (A) dorsal view; (B) ventral view, lateral abdominal musculature not shown complete; scale represents two millimeters; abbreviations given on pp. 4-7.

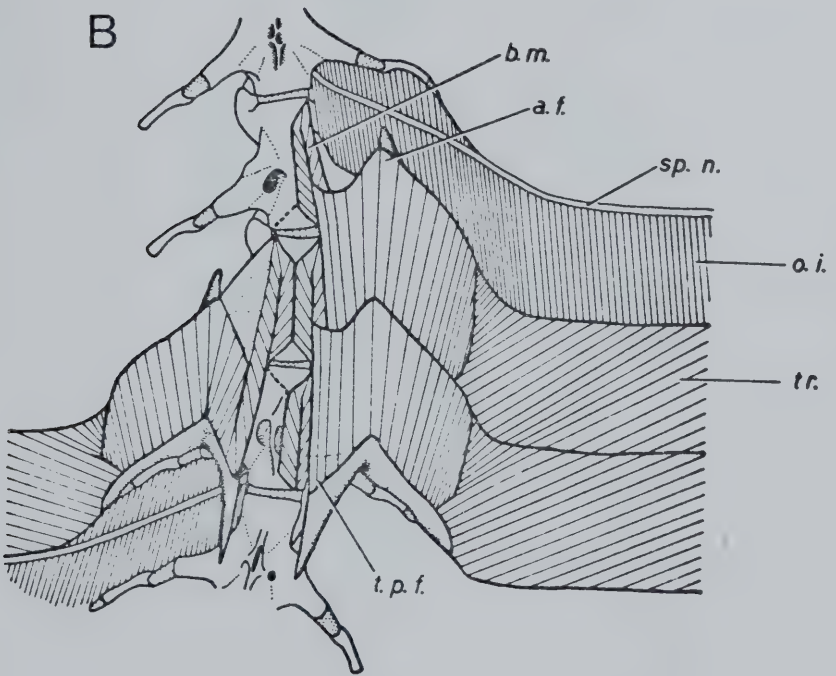
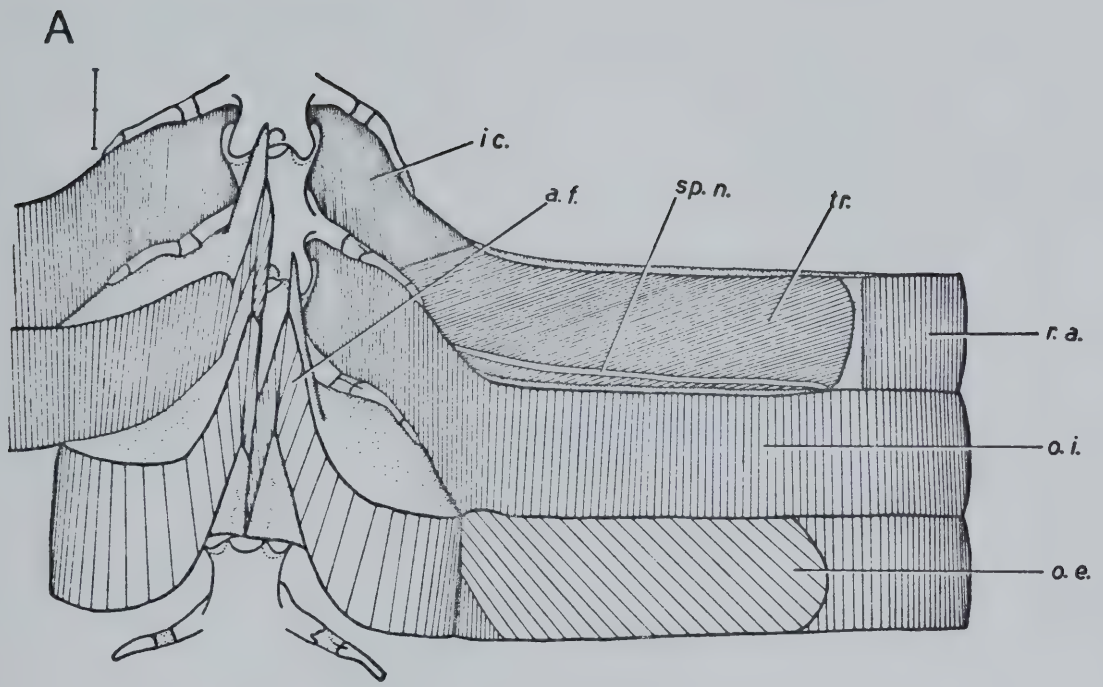


Figure 28. Dissection of the axial musculature of *Amphiuma tridactylum* with the lateral abdominal musculature removed: (A) lateral view; (B) dorsal view; scale represents two millimeters; abbreviations given on pp. 4-7.

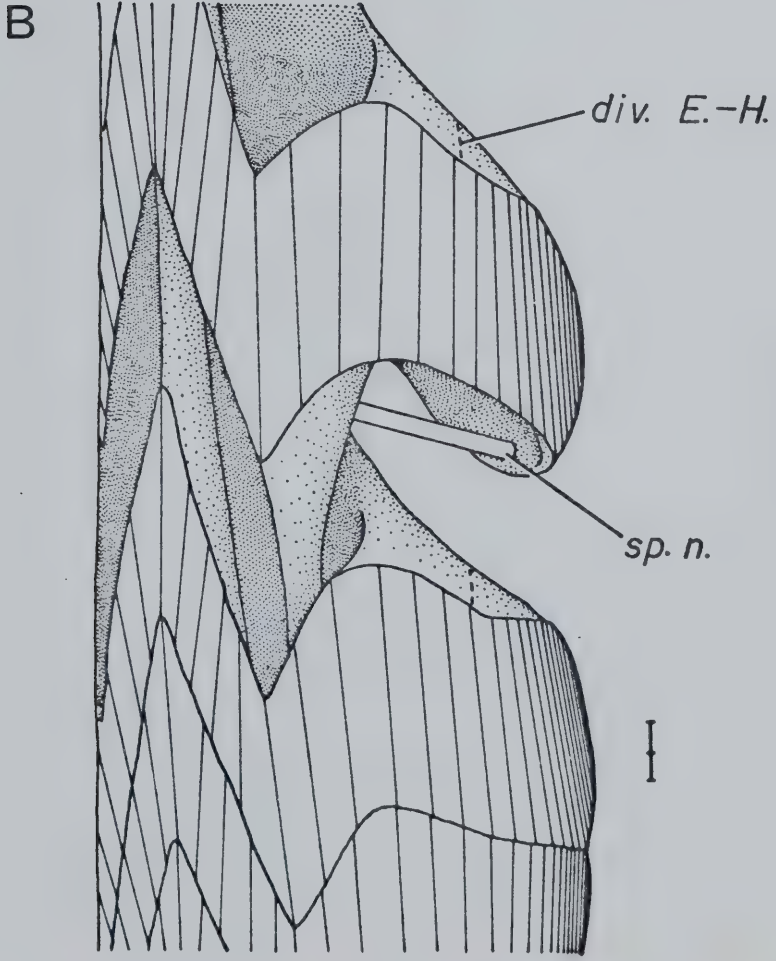
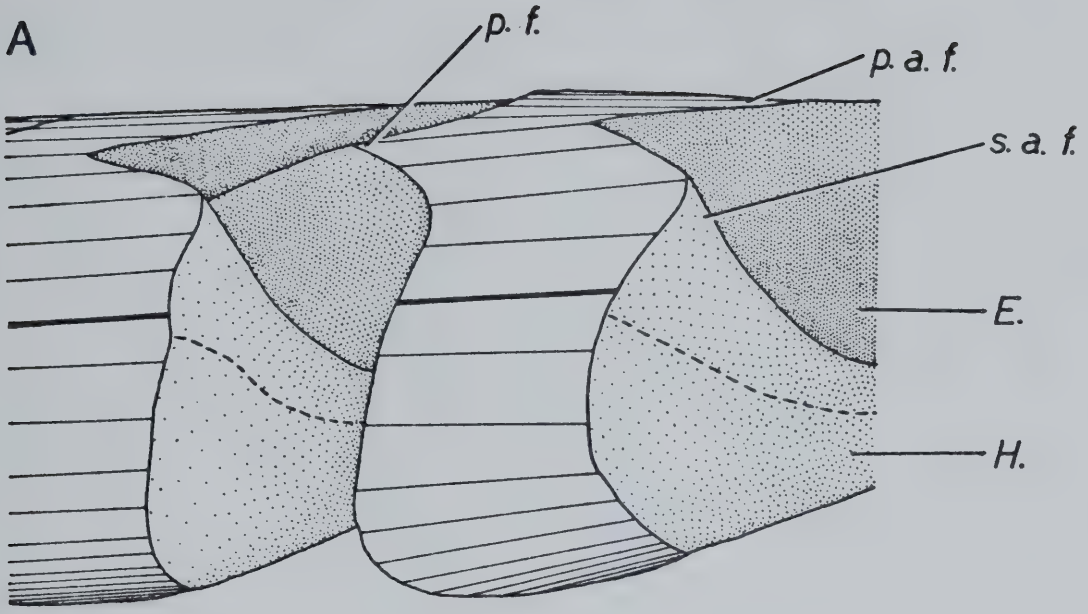


Figure 29. Dissection of the epaxial musculature of *Amphiuma tridactylum* in dorsal views: (A) superficial unit; (B) deeper units, labelling following Auffenberg (1959); scale represents two millimeters; abbreviations given on pp. 4-7.

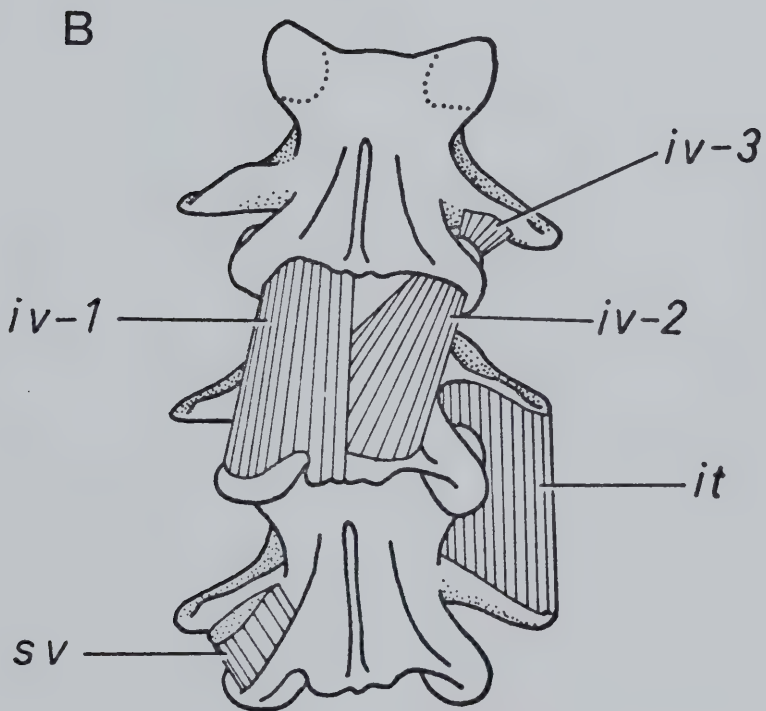
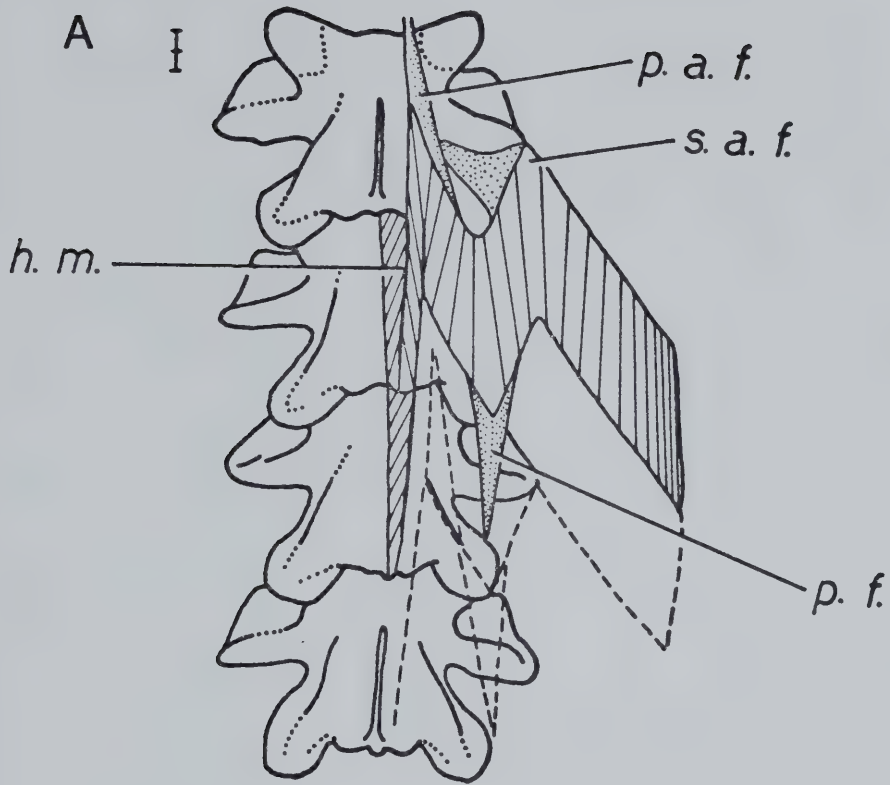


Figure 30. Dissection of the *subvertebralis* of *Amphiuma tri-dactylum* in ventral view; abbreviations given on pp. 4-7.

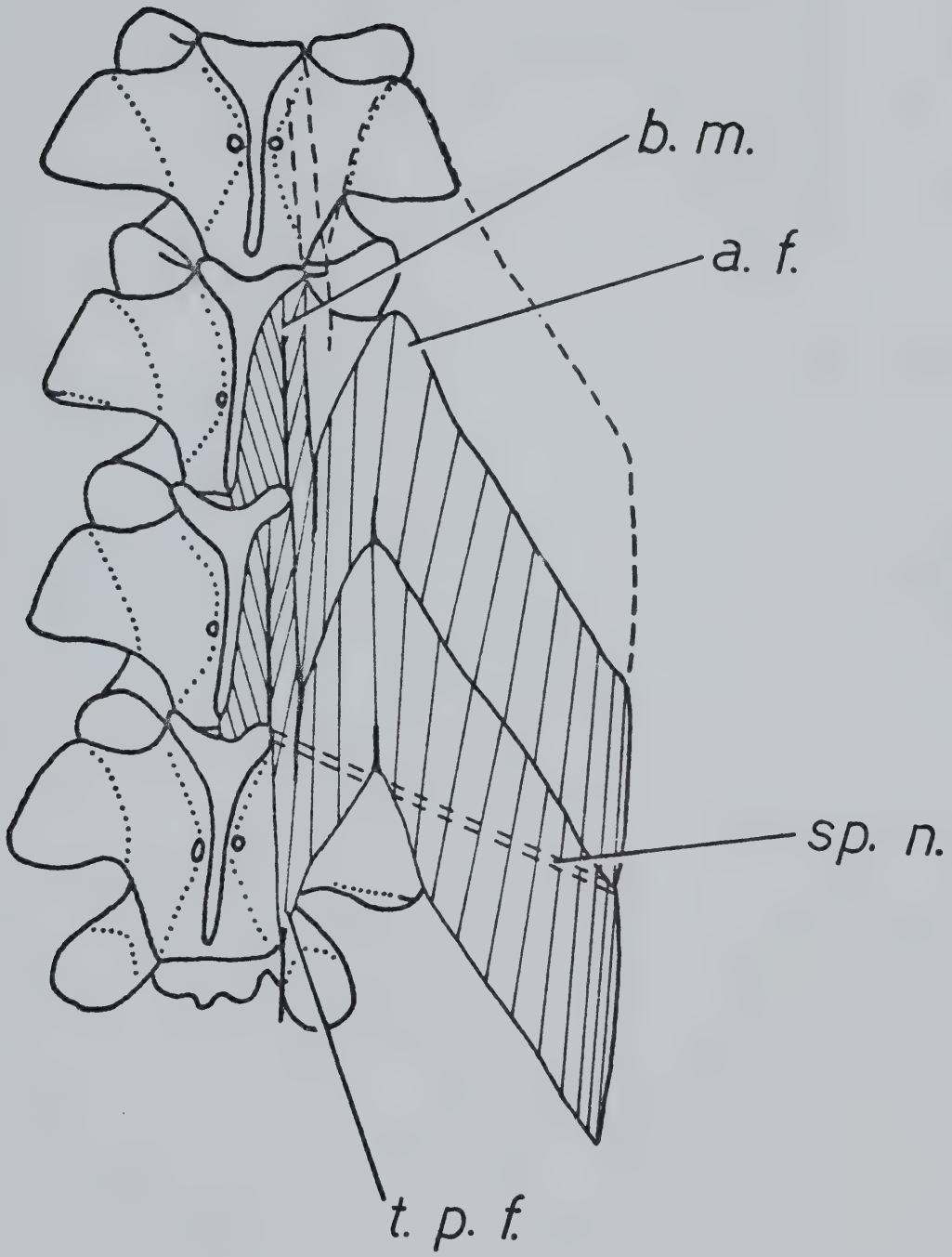


Figure 31. Lateral abdominal musculature of *Amphiuma tridactylum*
in lateral view; scale represents two millimeters;
abbreviations given on pp. 4-7.

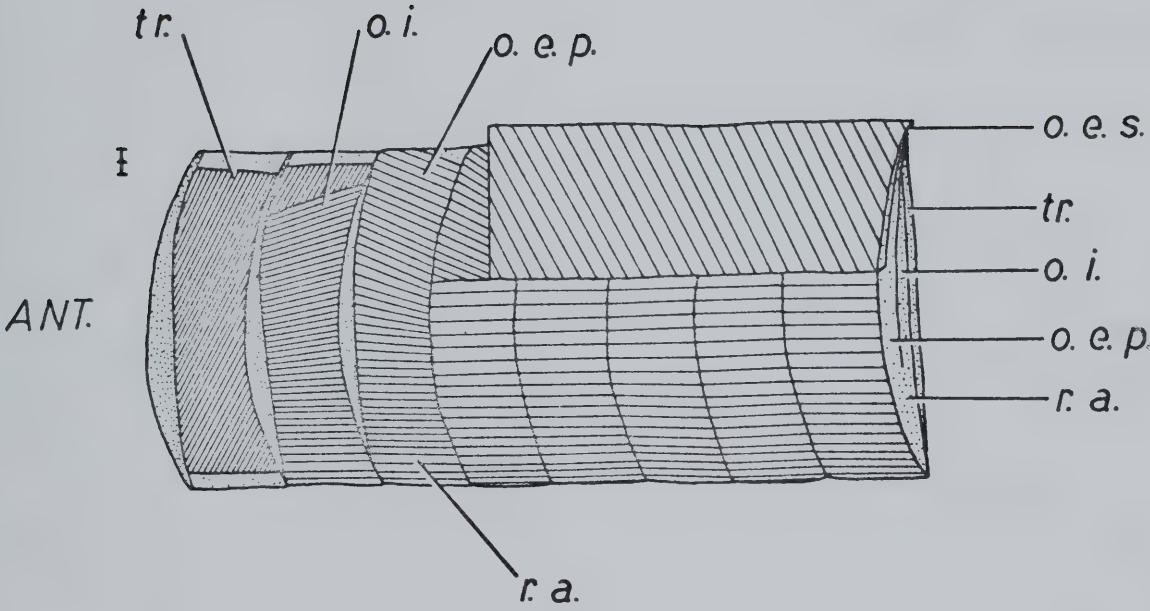


Figure 32. Cross-section through the trunk musculature of *Amphiana tridactylum*; scale represents two millimeters; abbreviations given on pp. 4-7.

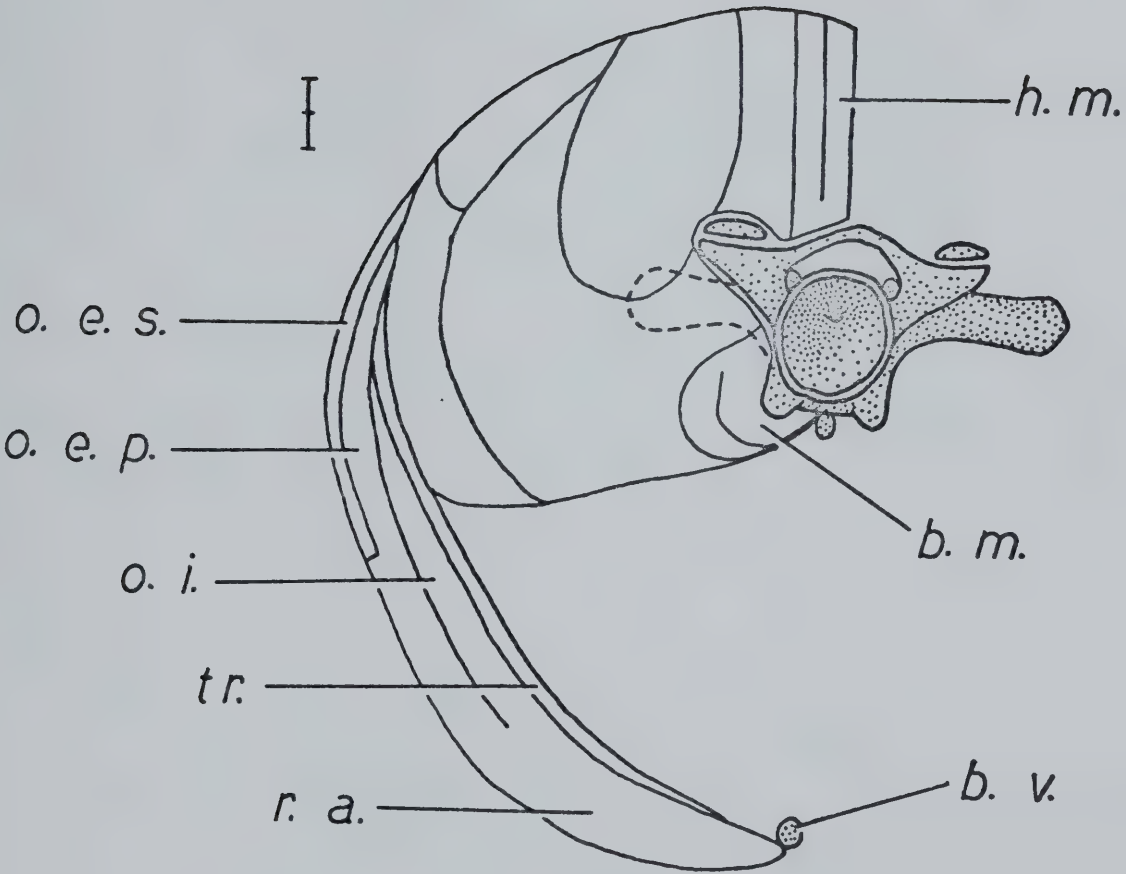


Figure 33. Dissection of larval *Dicamptodon ensatus* with lateral abdominal musculature spread laterally: (A) dorsal view; (B) ventral view; scale represents two millimeters; abbreviations given on pp. 4-7.

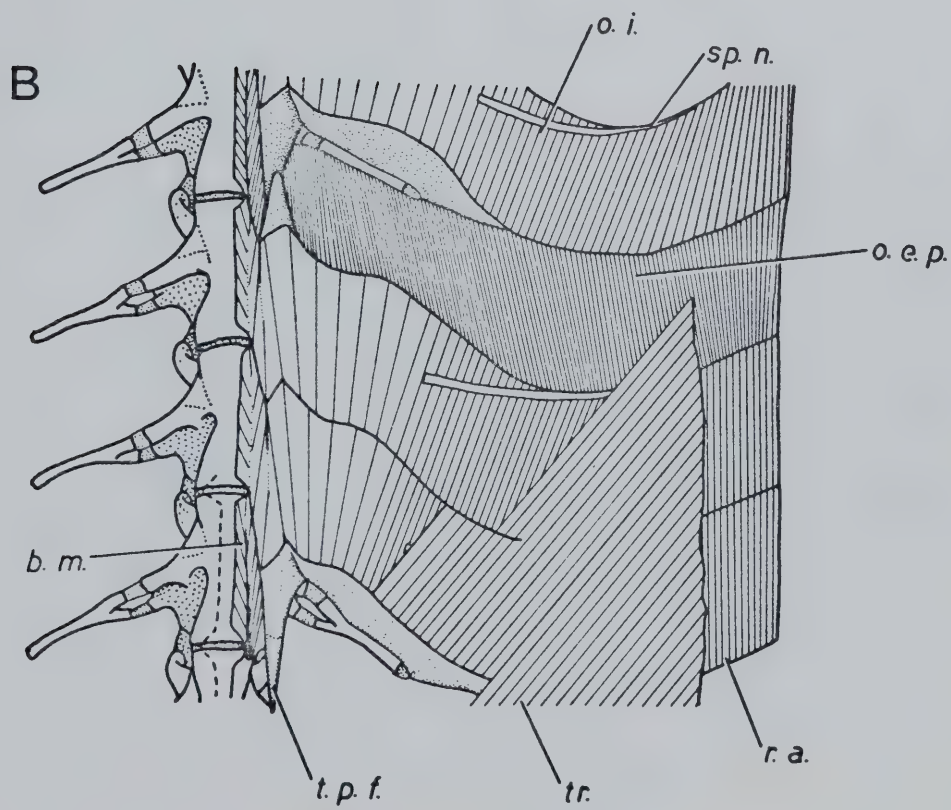
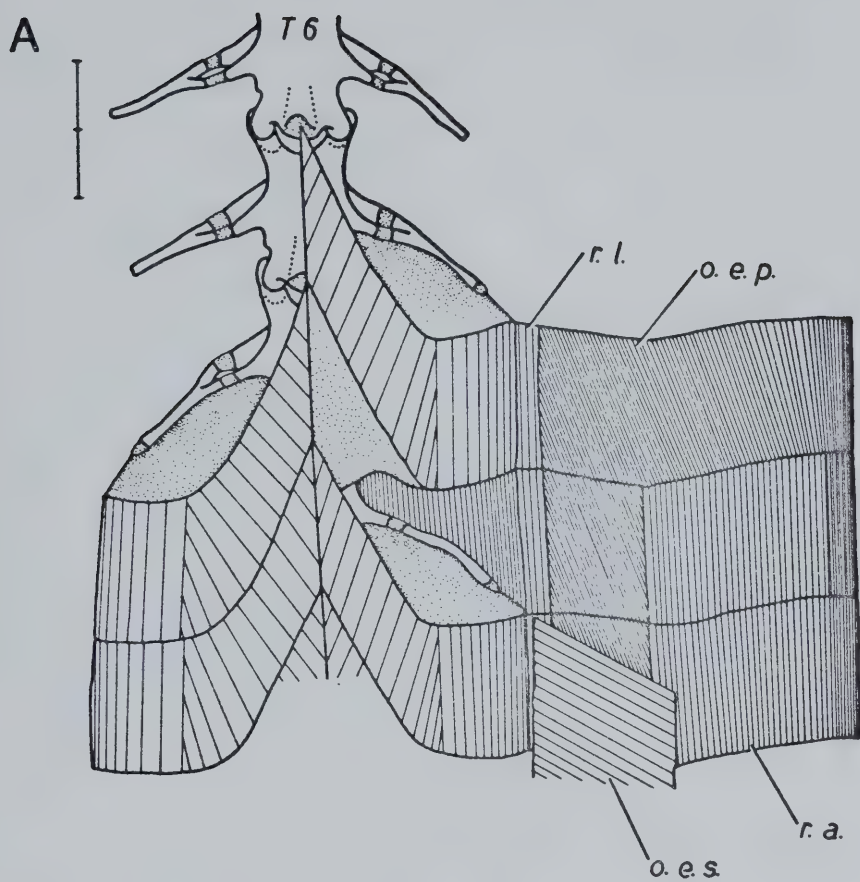


Figure 34. Dissection of metamorphosed adult *Dicamptodon ensatus* with lateral abdominal musculature spread laterally: (A) dorsal view; (B) ventral view; scale represents two millimeters; abbreviations given on pp. 4-7.

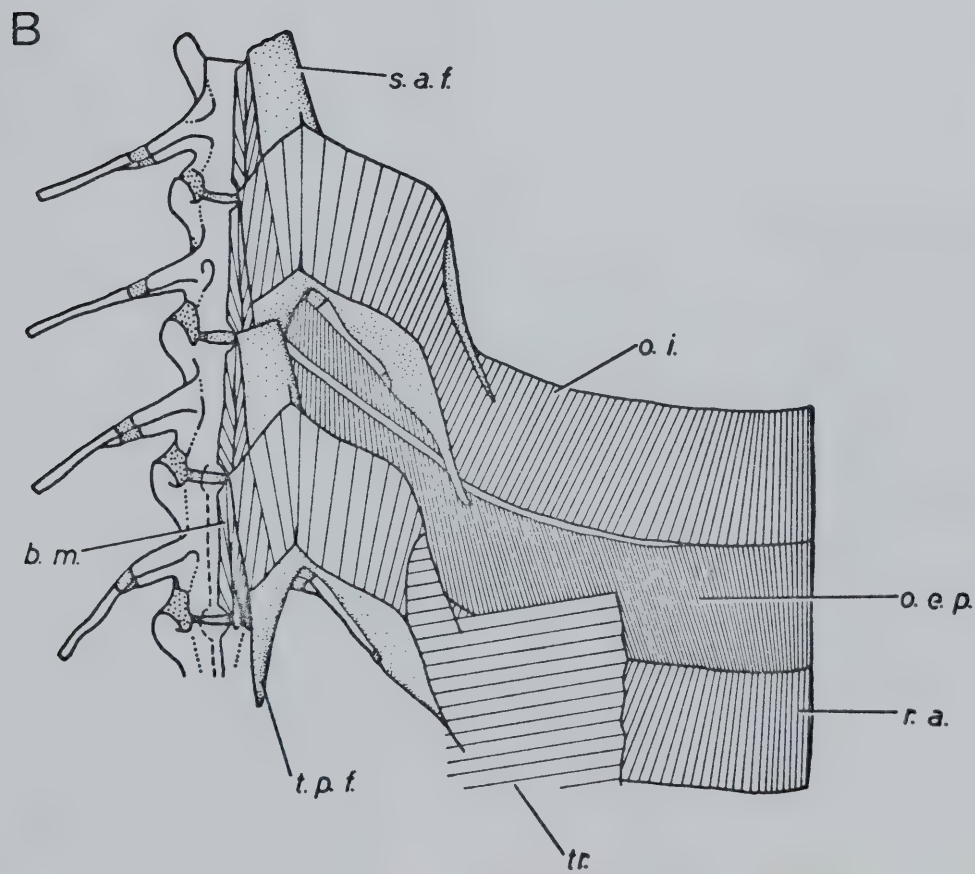
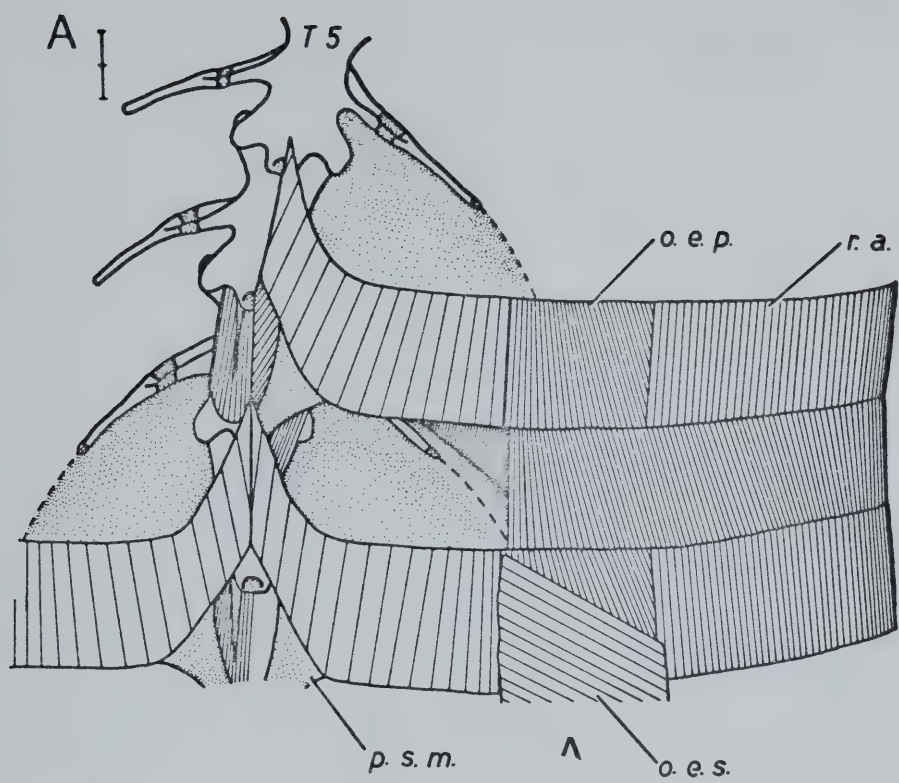


Figure 35. Dissection of *Rhyacotriton olympicus* with lateral abdominal musculature spread laterally: (A) dorsal view; (B) ventral view; scale represents two millimeters; abbreviations given on pp. 4-7.

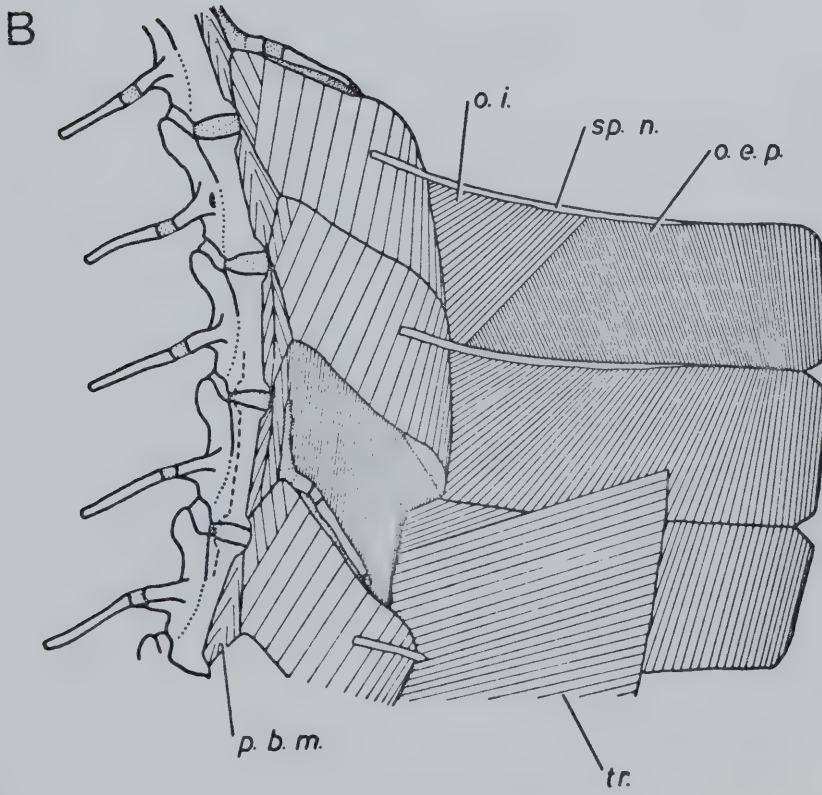
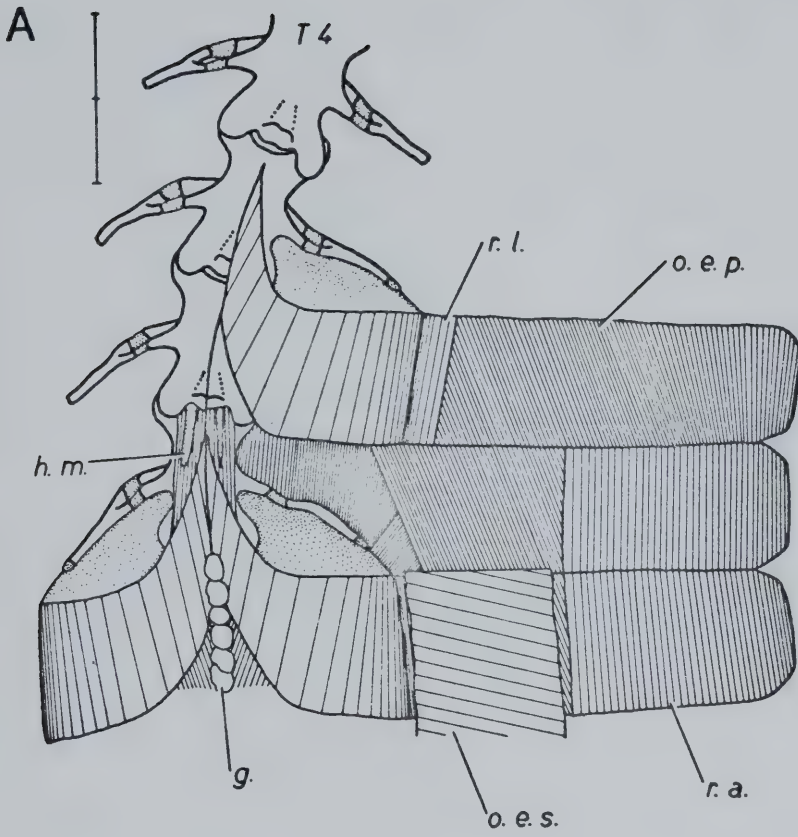


Figure 36. Dissection of *Ambystoma macrodactylum* with lateral abdominal musculature spread laterally: (A) dorsal view; (B) ventral view; scale represents two millimeters; abbreviations given on pp. 4-7.

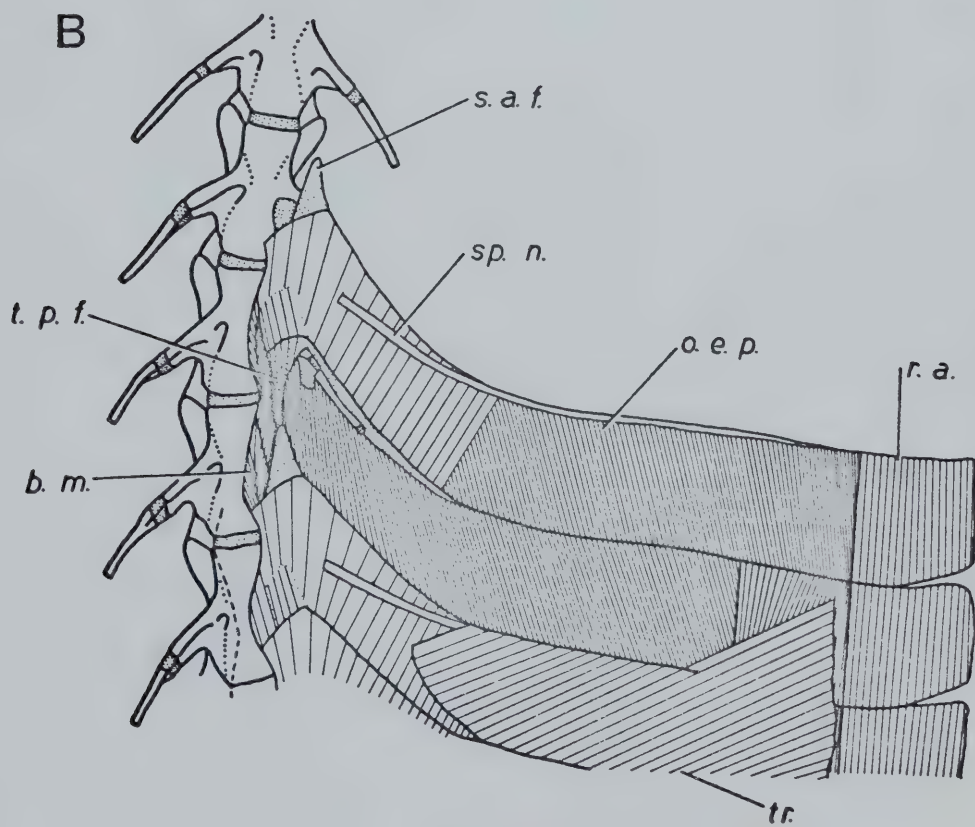
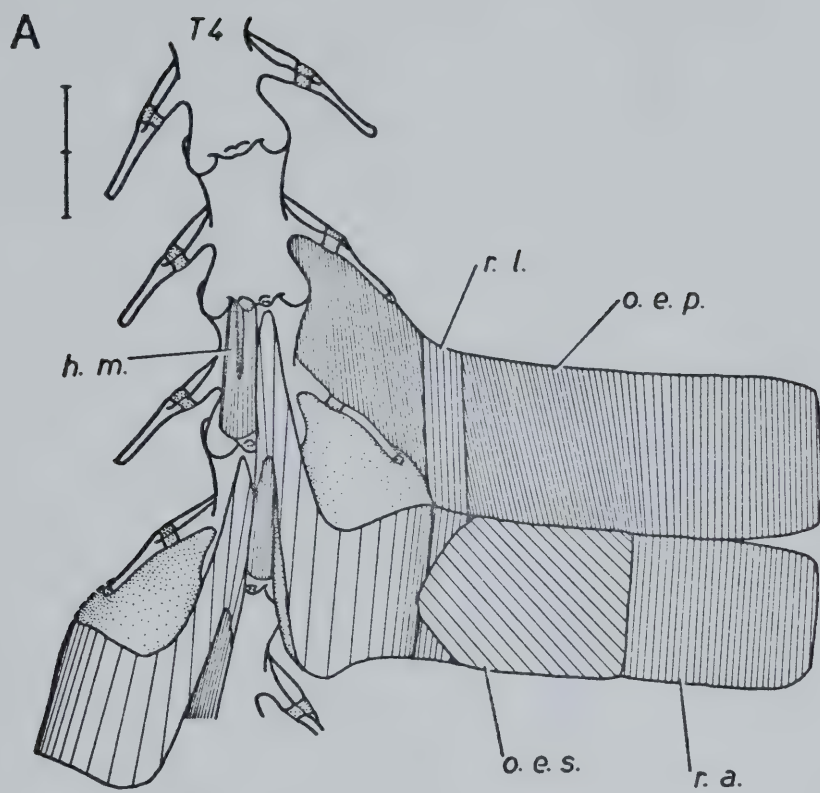


Figure 37. Partial dissection of the trunk musculature of a larval *Ambystoma gracile* in lateral view; scale represents two millimeters; abbreviations given on pp. 4-7.

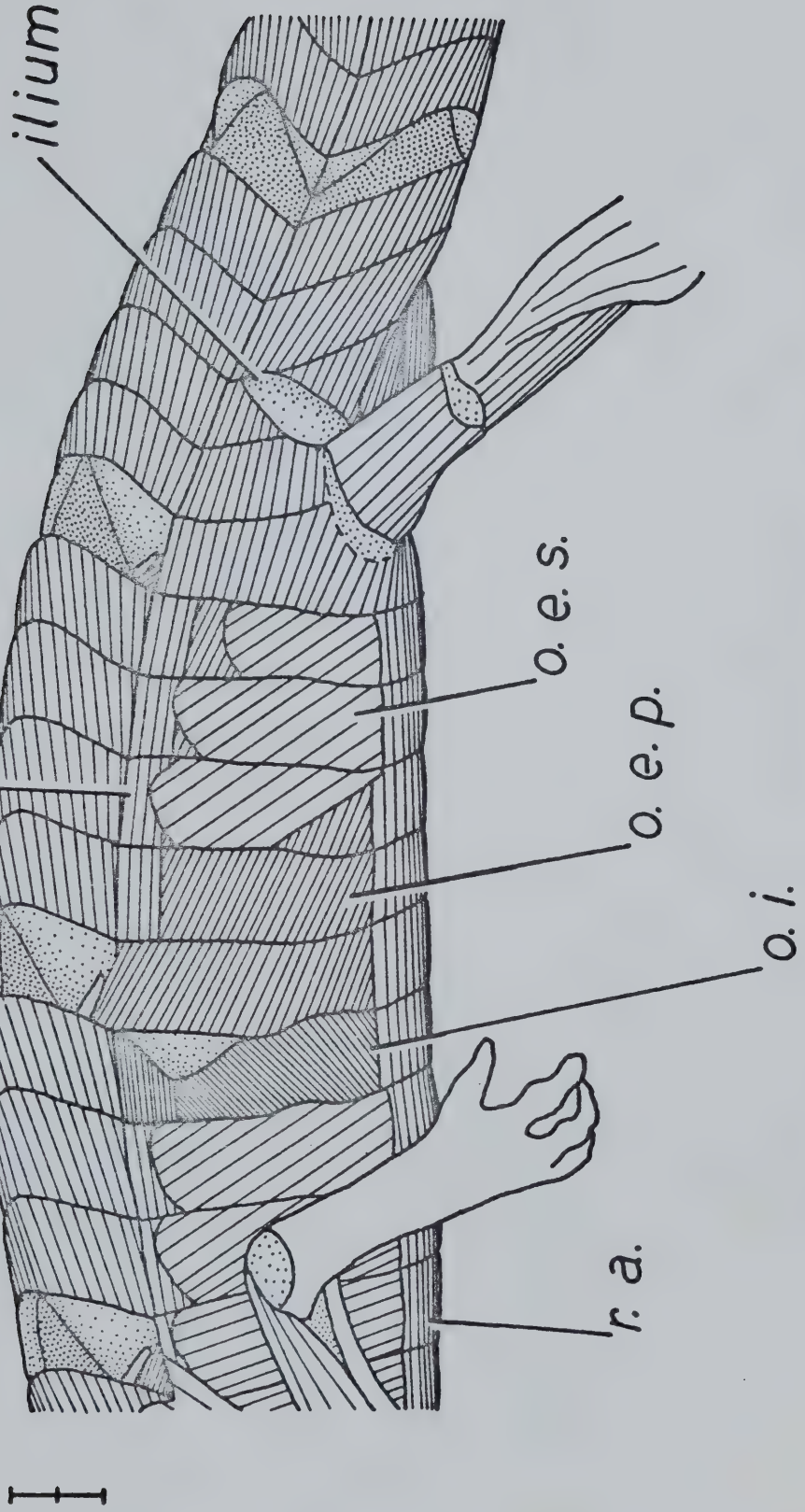


Figure 38. Dissection of larval *Ambystoma gracile* with lateral abdominal musculature spread laterally: (A) dorsal view; lateral abdominal musculature not shown complete; (B) ventral view; scale represents two millimeters; abbreviations given on pp. 4-7.

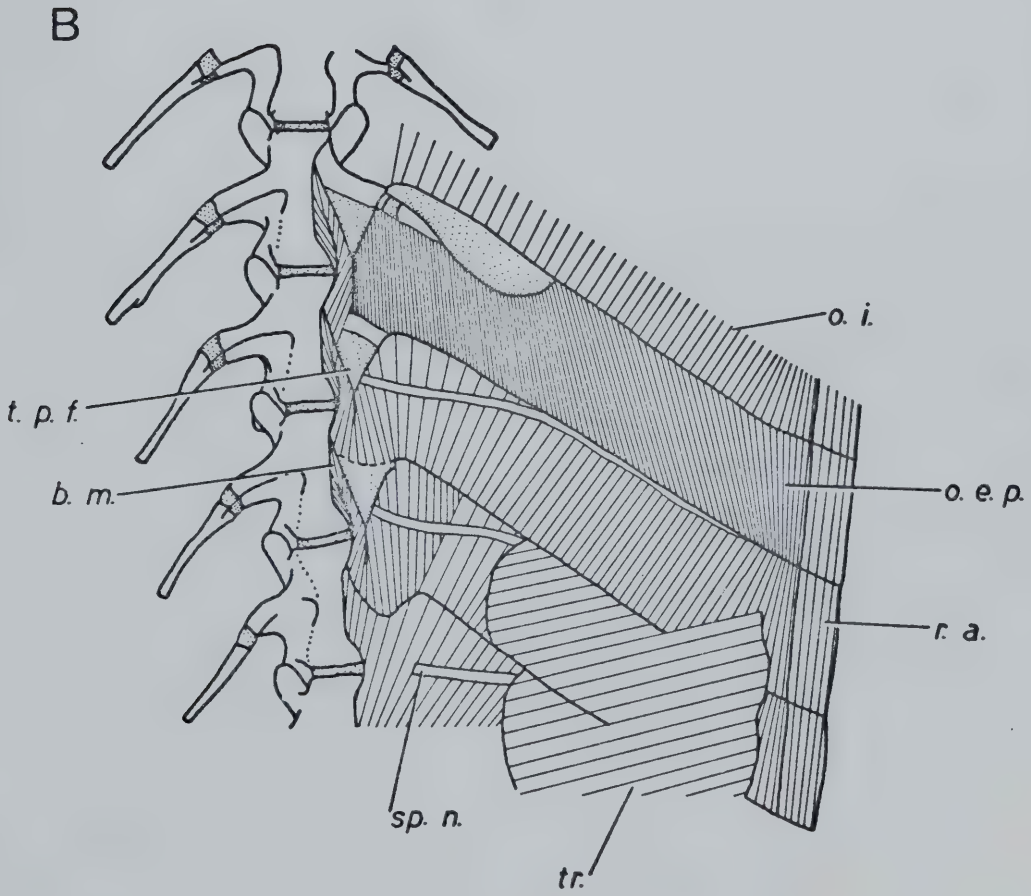
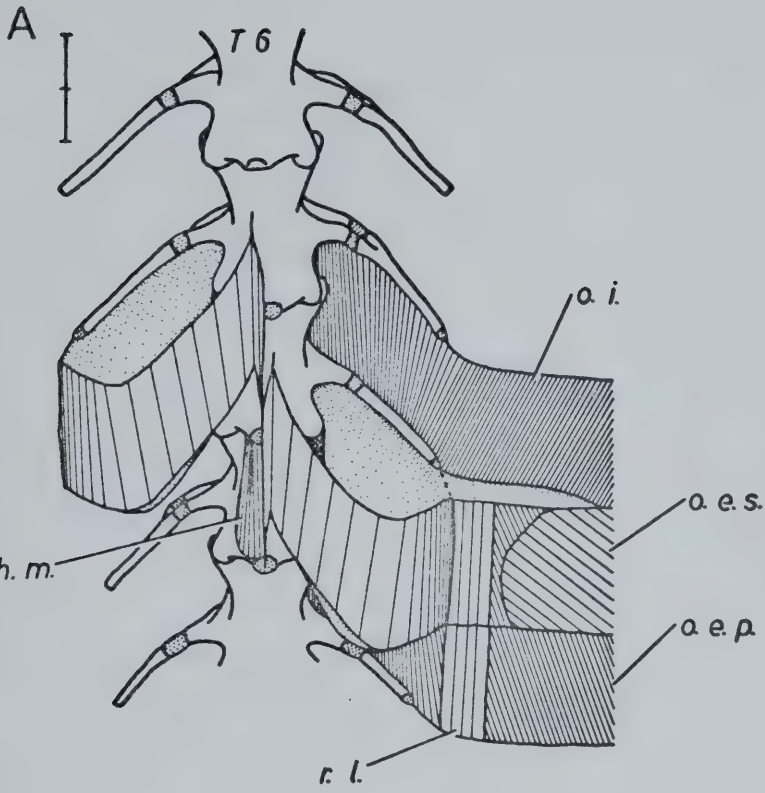


Figure 39. Dissection of *Ambystoma maculatum* with lateral abdominal musculature spread laterally: (A) dorsal view; (B) ventral view; scale represents two millimeters; abbreviations given on pp. 4-7.

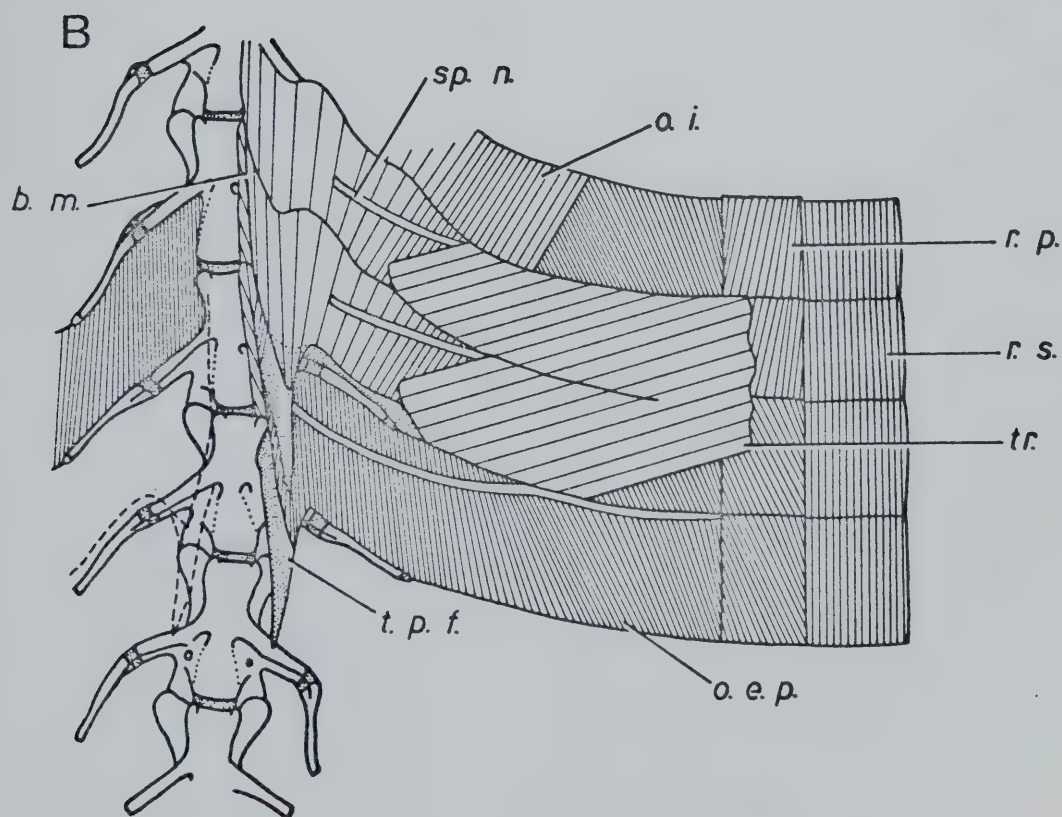
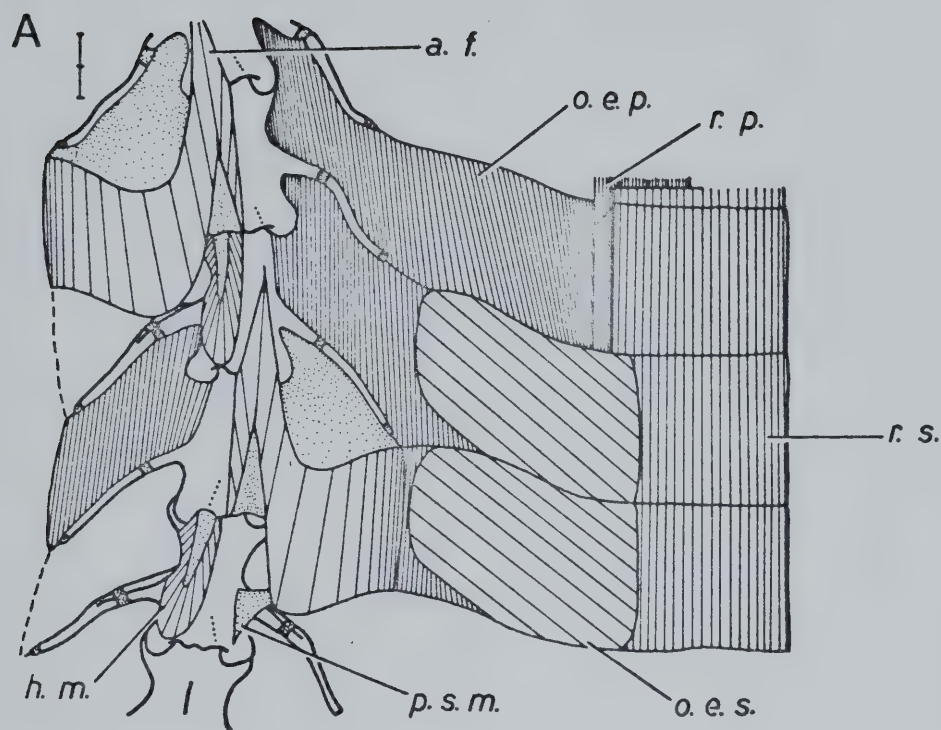


Figure 40. Dissection of *Ambystoma jeffersonianum* with lateral abdominal musculature spread laterally: (A) dorsal view; (B) ventral view; scale represents one millimeter; abbreviations given on pp. 4-7.

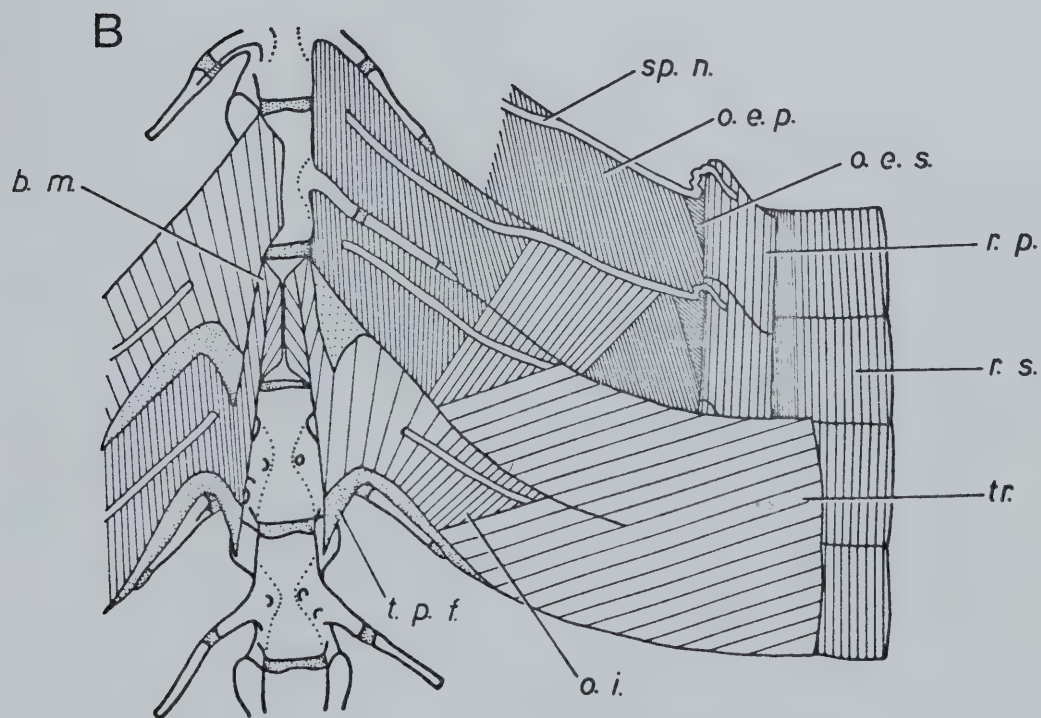
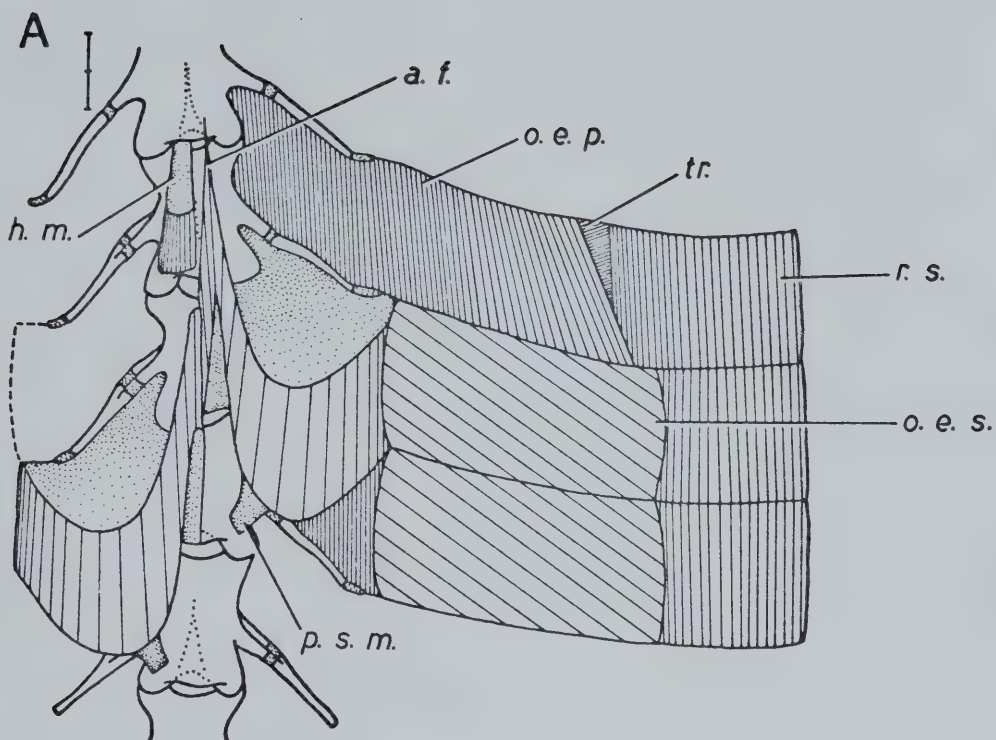


Figure 41. Dissection of *Ambystoma opacum* with lateral abdominal musculature spread laterally: (A) dorsal view; (B) ventral view; scale represents two millimeters; abbreviations given on pp. 4-7.

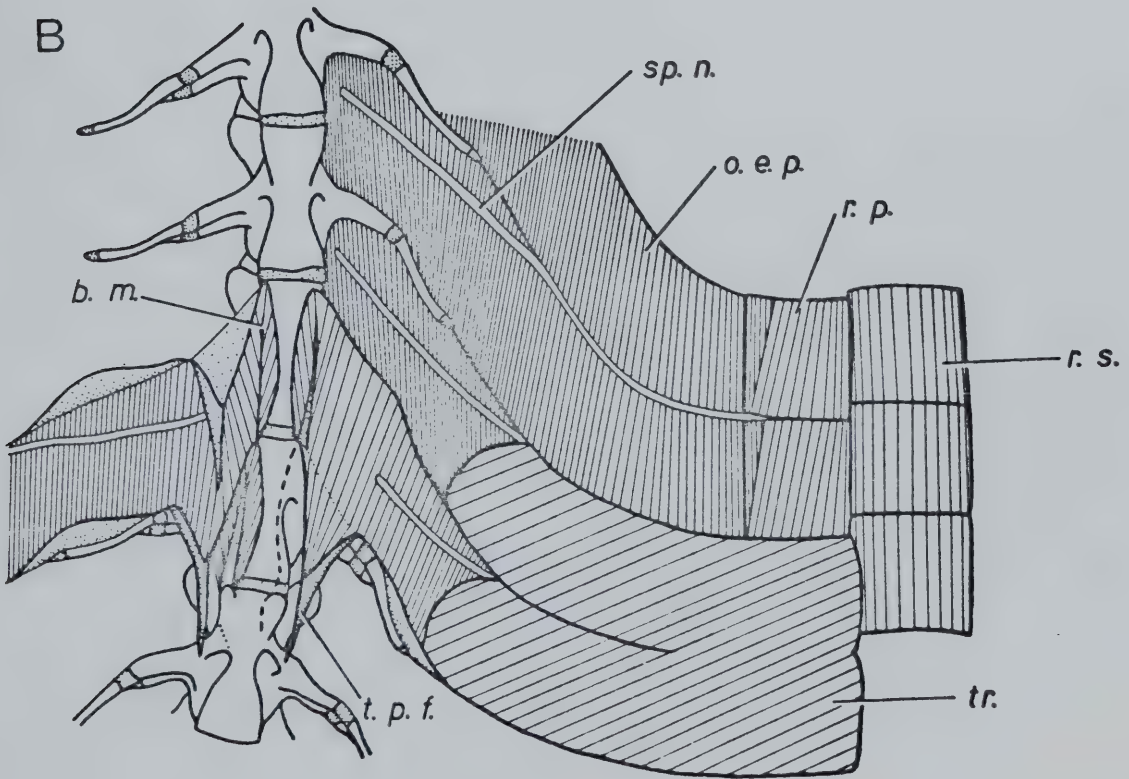
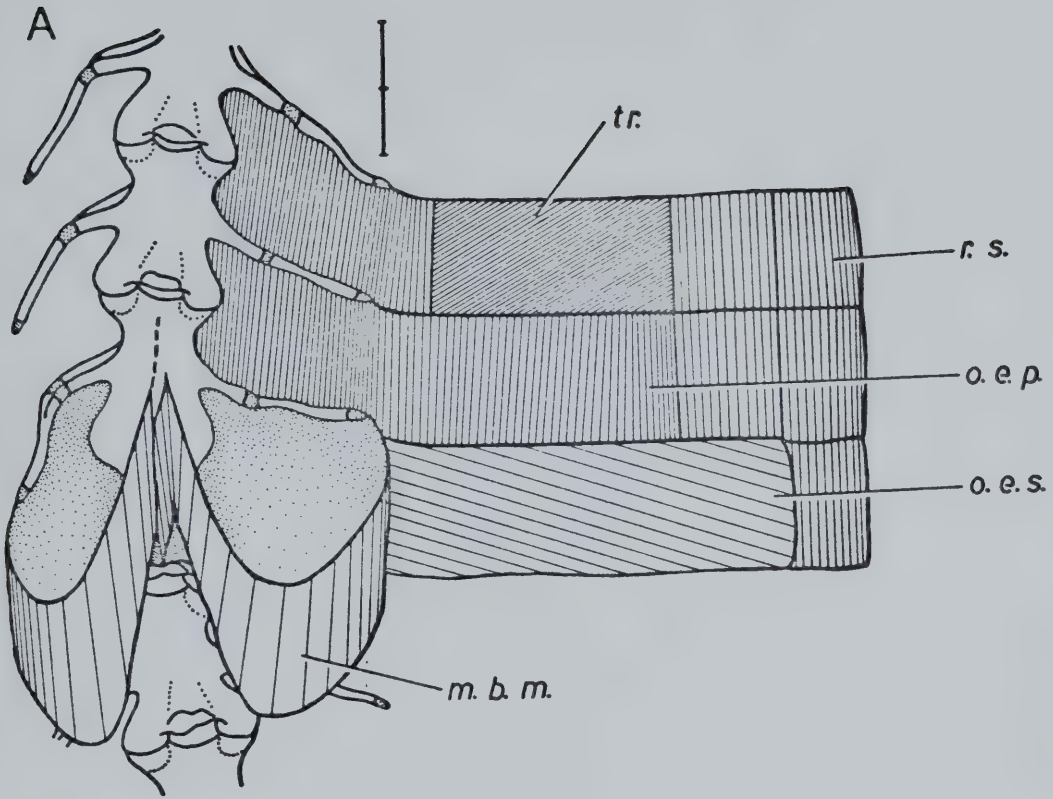
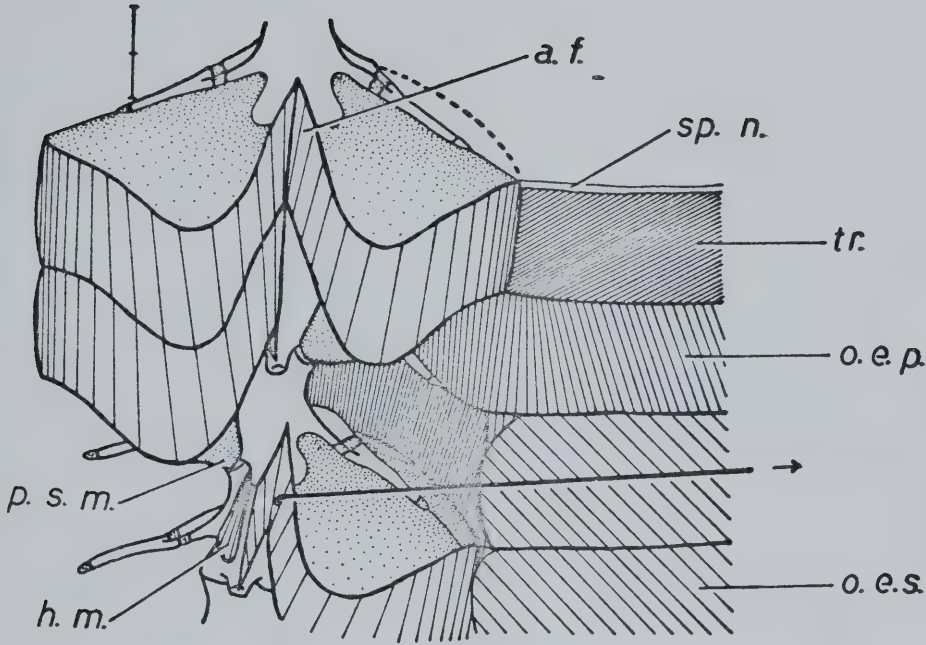


Figure 42. Dissection of *Ambystoma talpoideum* with lateral abdominal musculature spread laterally: (A) dorsal view; (B) ventral view; scale represents two millimeters; abbreviations given on pp. 4-7.

A



B

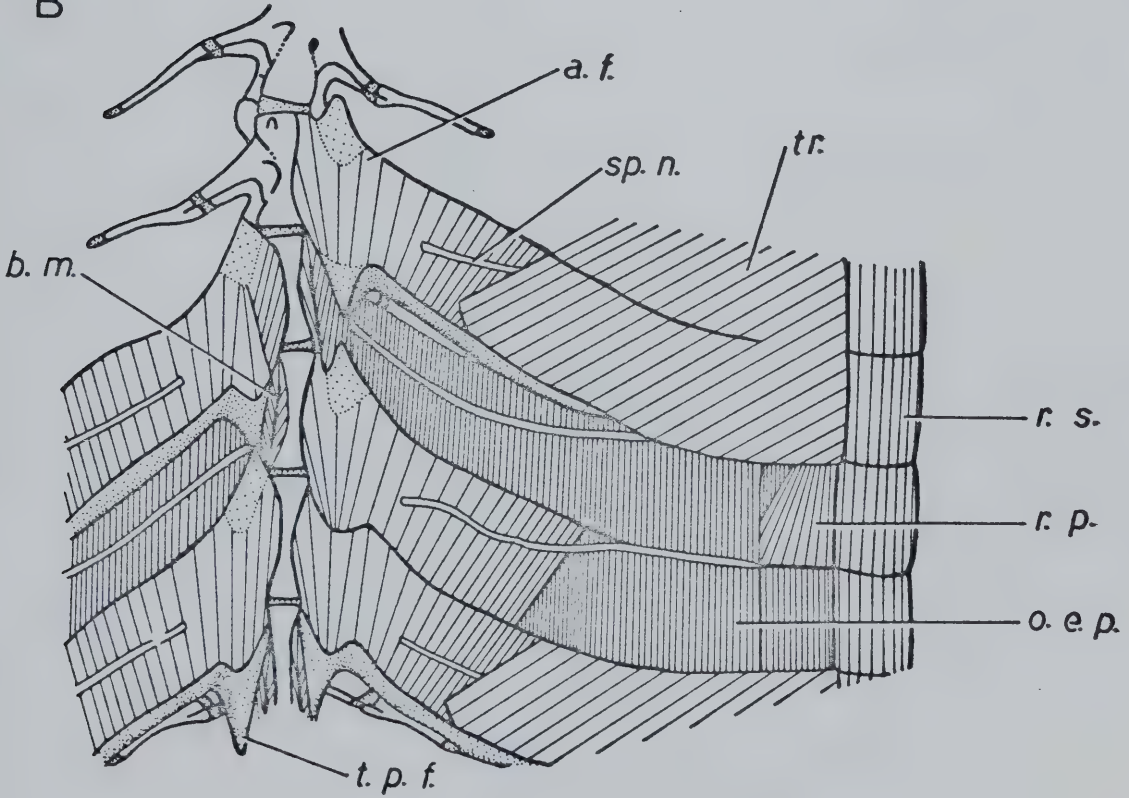


Figure 43. Dissection of larval *Ambystoma tigrinum* with lateral abdominal musculature not shown complete: (A) dorsal view; (B) ventral view; scale represents two millimeters; abbreviations given on pp. 4-7.

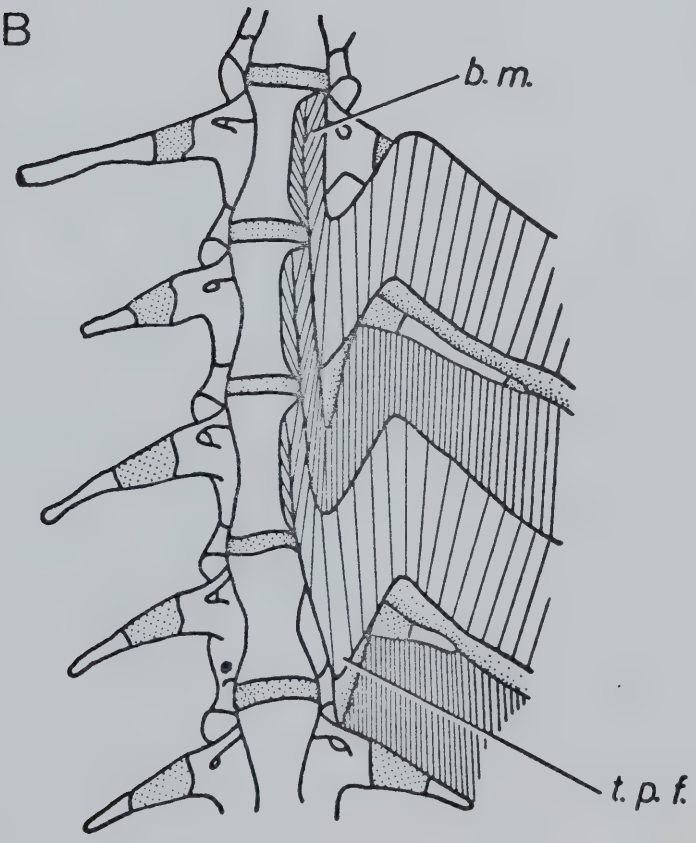
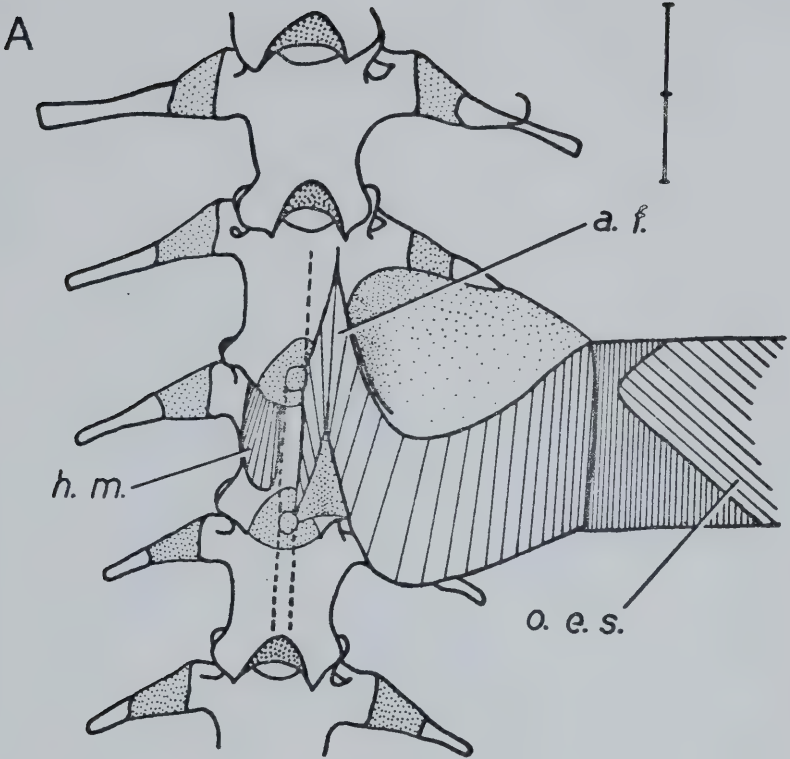


Figure 44. Dissection of young metamorphosed *Ambystoma tigrinum* with lateral abdominal musculature spread laterally: (A) dorsal view; (B) ventral view, lateral abdominal musculature not shown complete; scale represents two millimeters; abbreviations given on pp. 4-7.

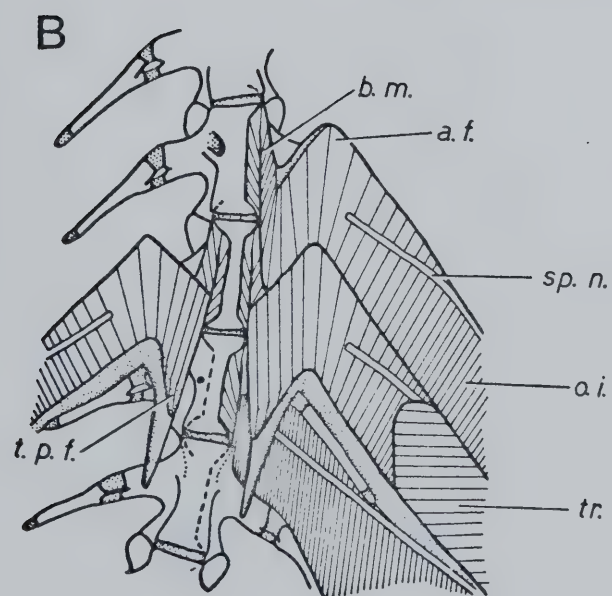
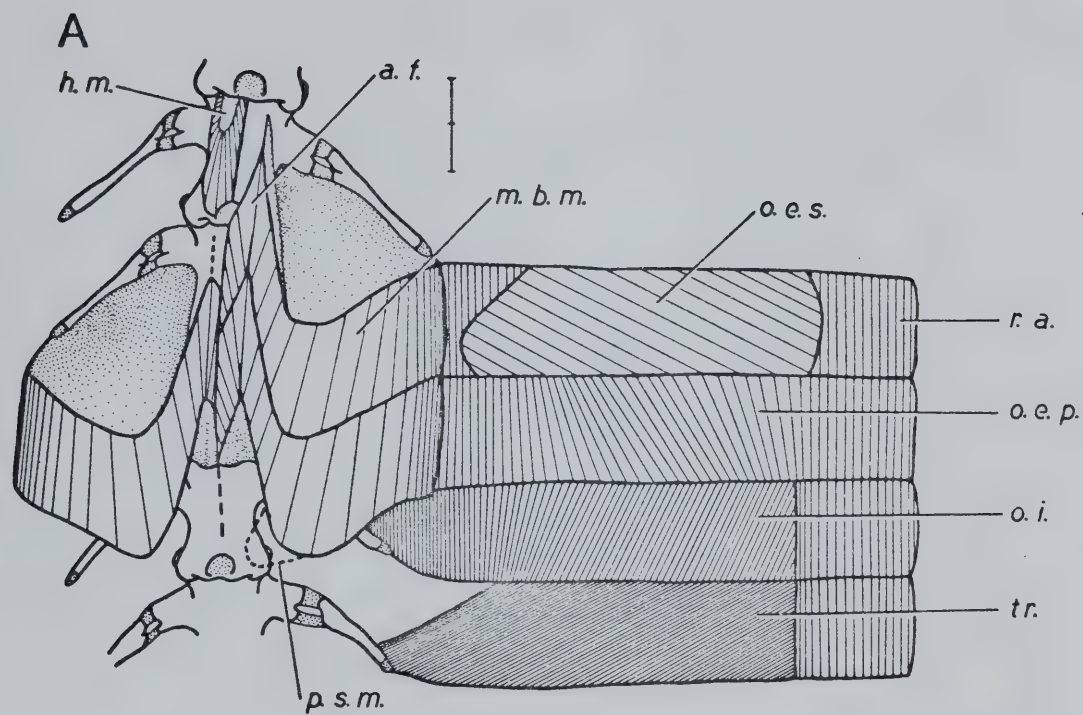
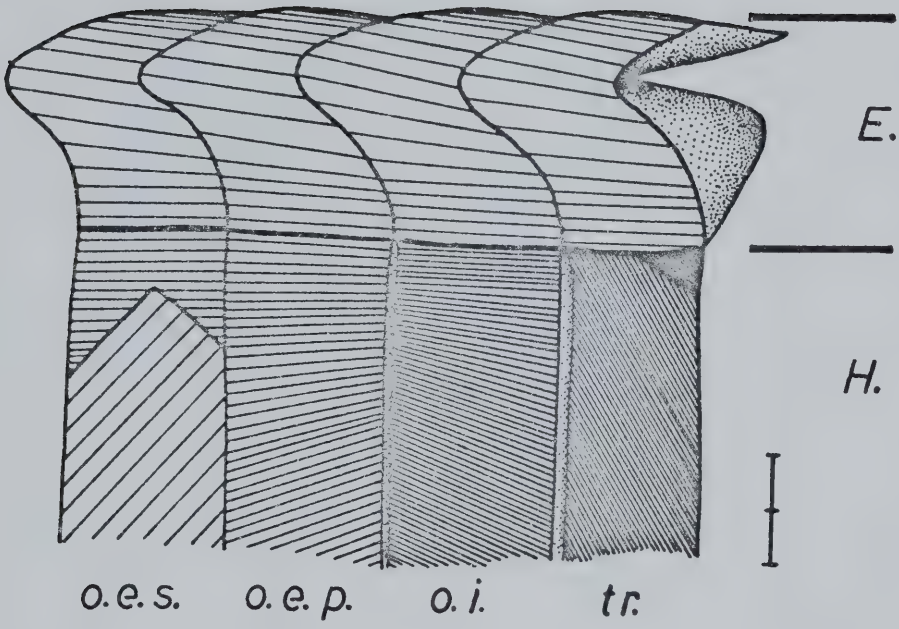


Figure 45. *Ambystoma tigrinum*: (A) lateral view of four segments of the trunk musculature; (B) trunk vertebrae in lateral view, showing position of the hyperapophyseal muscle; scales represent two millimeters; abbreviations given on pp. 4-7.

A



B

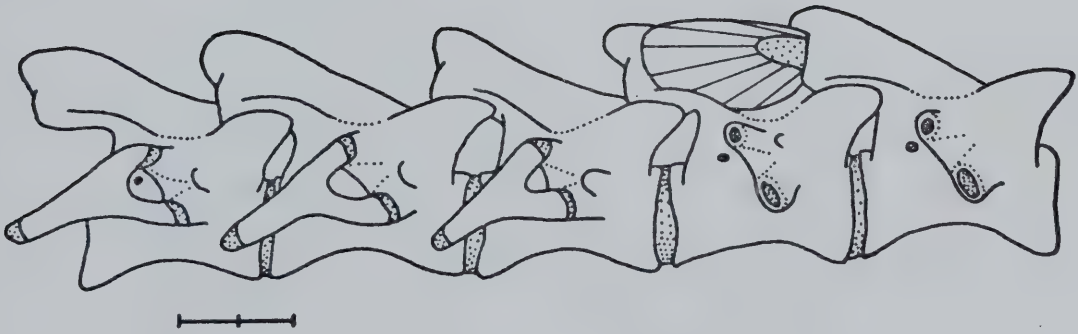


Figure 46. Dissection of *Necturus maculosus* with lateral abdominal musculature spread laterally: (A) dorsal view, lateral abdominal musculature not shown complete; (B) ventral view; scale represents two millimeters; abbreviations given on pp. 4-7.

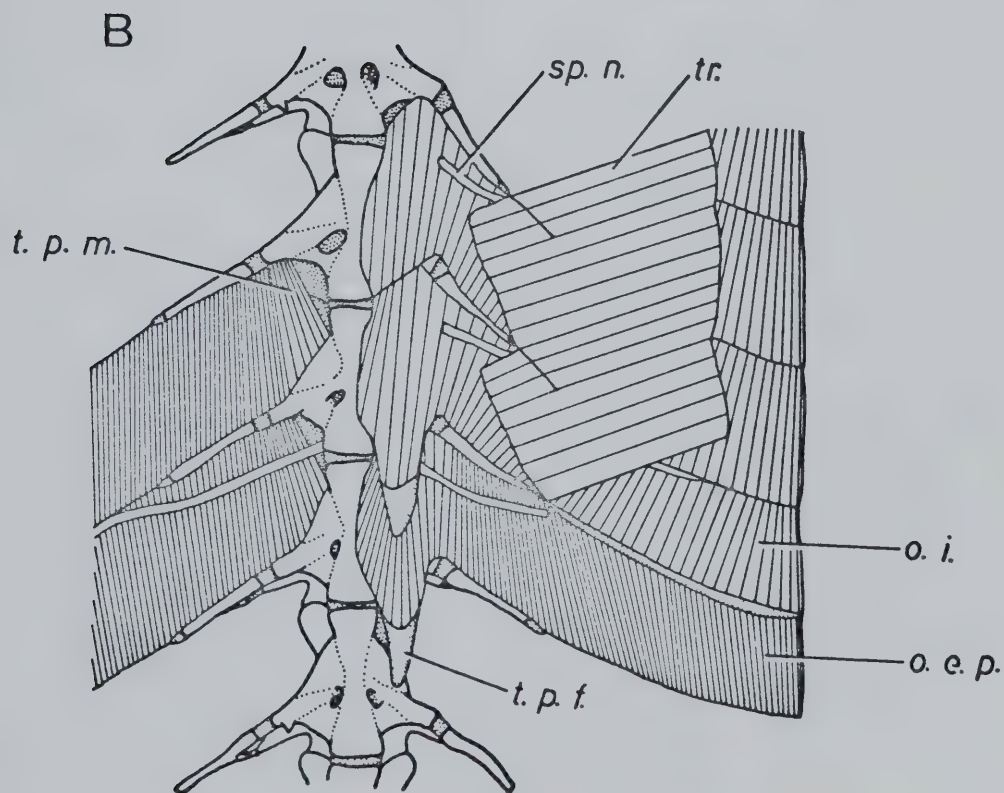
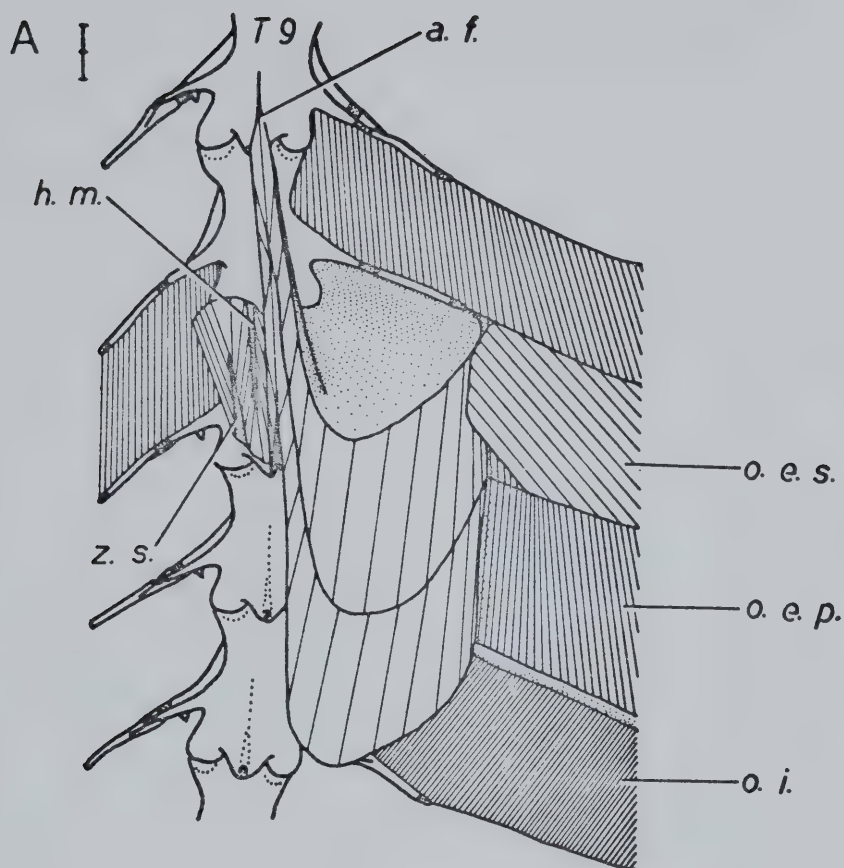


Figure 47. Cross-sections through the trunk musculature of
(A) *Cryptobranchus alleganiensis*; (B) *Necturus*
maculosus; abbreviations given on pp. 4-7.

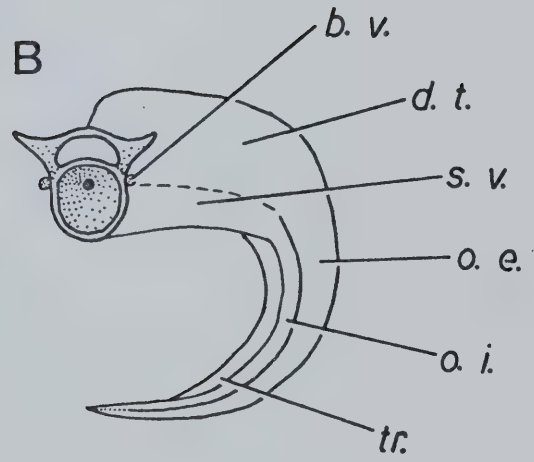
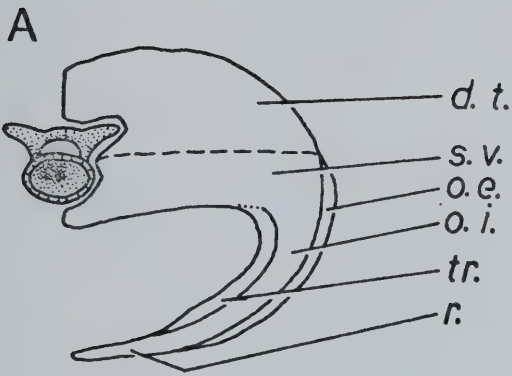


Figure 48. Partial dissection of the trunk musculature of *Proteus anguinus* in lateral view; scale represents two millimeters; abbreviations given on pp. 4-7.

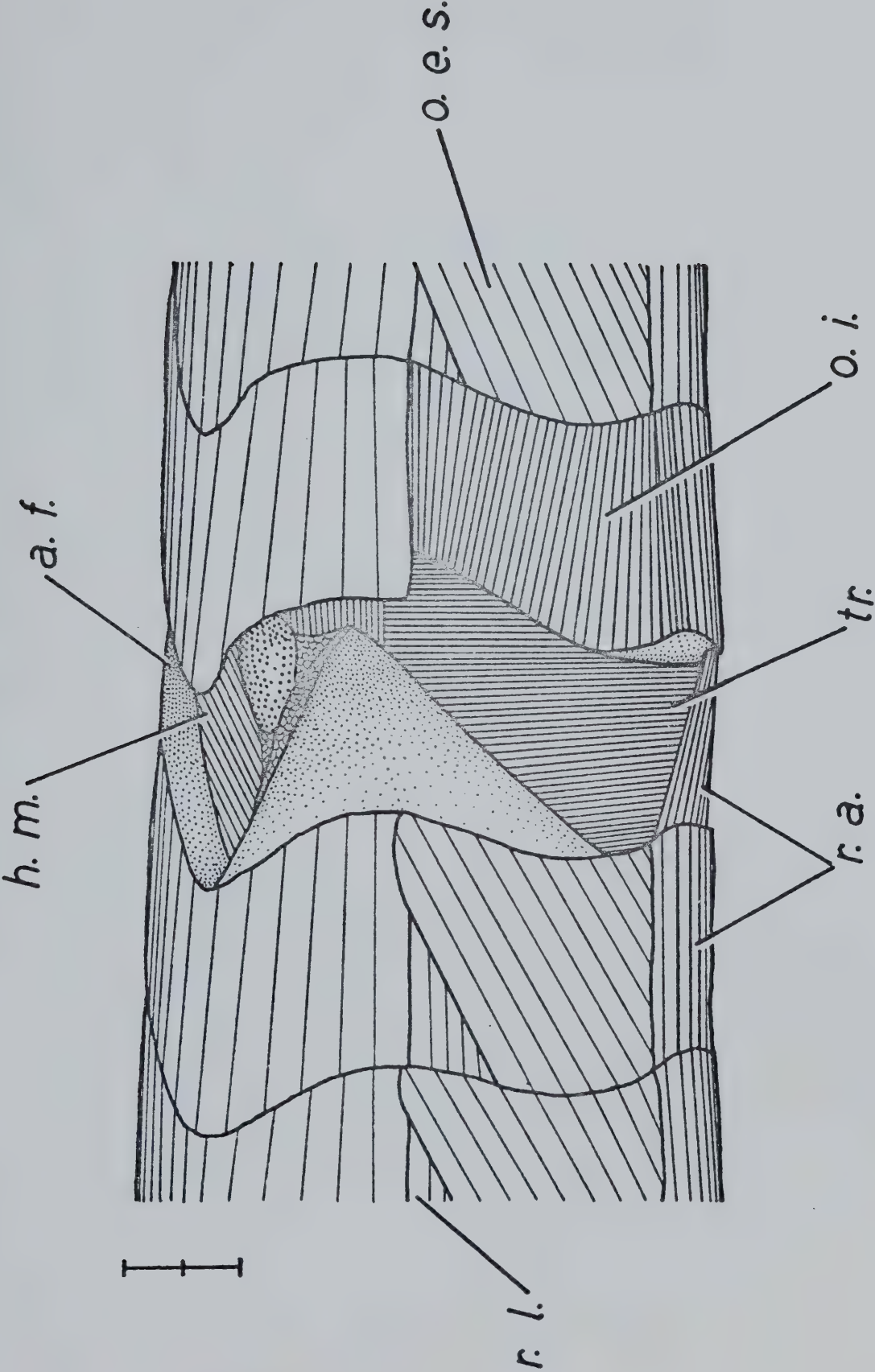
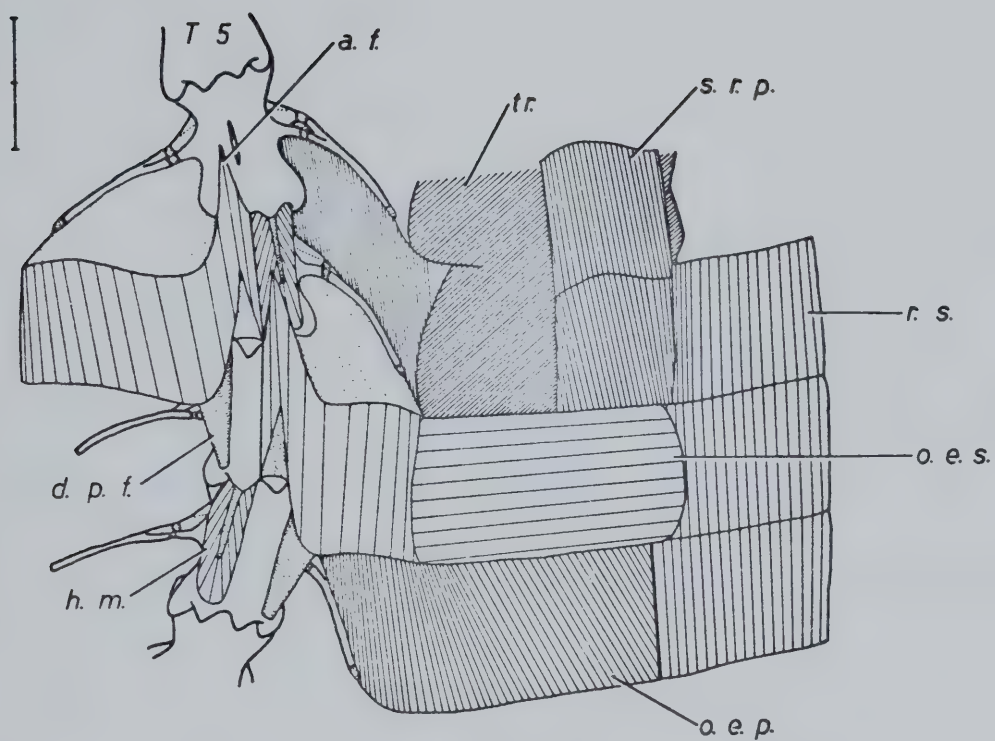


Figure 49. Dissection of *Plethodon jordani* with lateral abdominal musculature spread laterally: (A) dorsal view; (B) ventral view; scale represents two millimeters; abbreviations given on pp. 4-7.

A



B

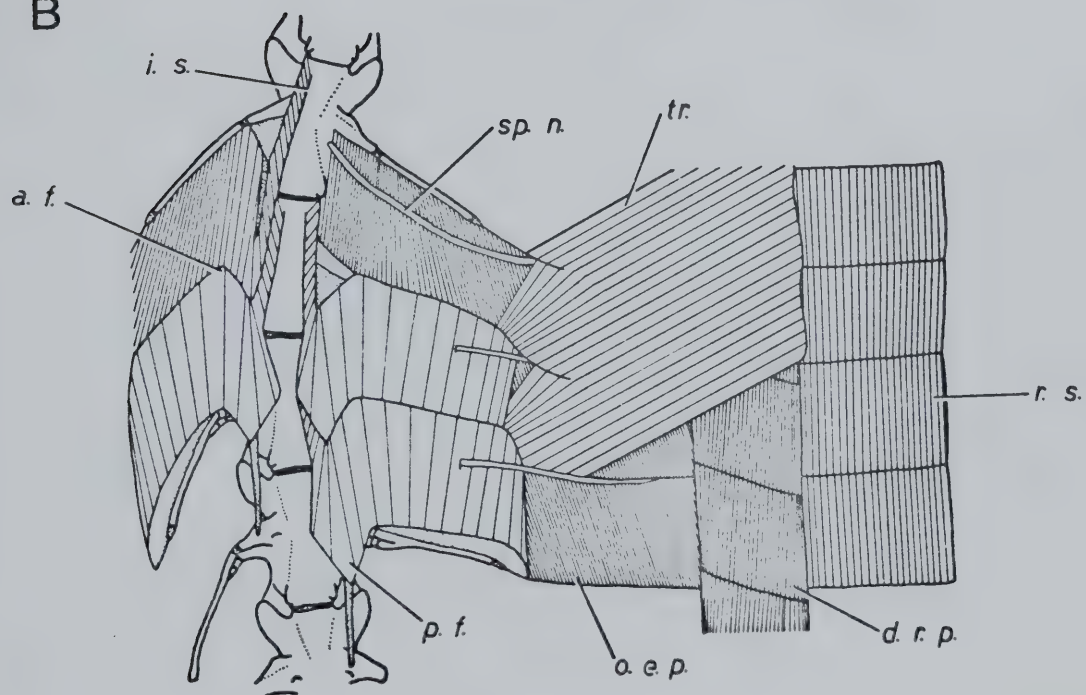


Figure 50. Dissection of *Plethodon glutinosus* with lateral abdominal musculature spread laterally: (A) dorsal view; (B) ventral view; scale represents two millimeters; abbreviations given on pp. 4-7.

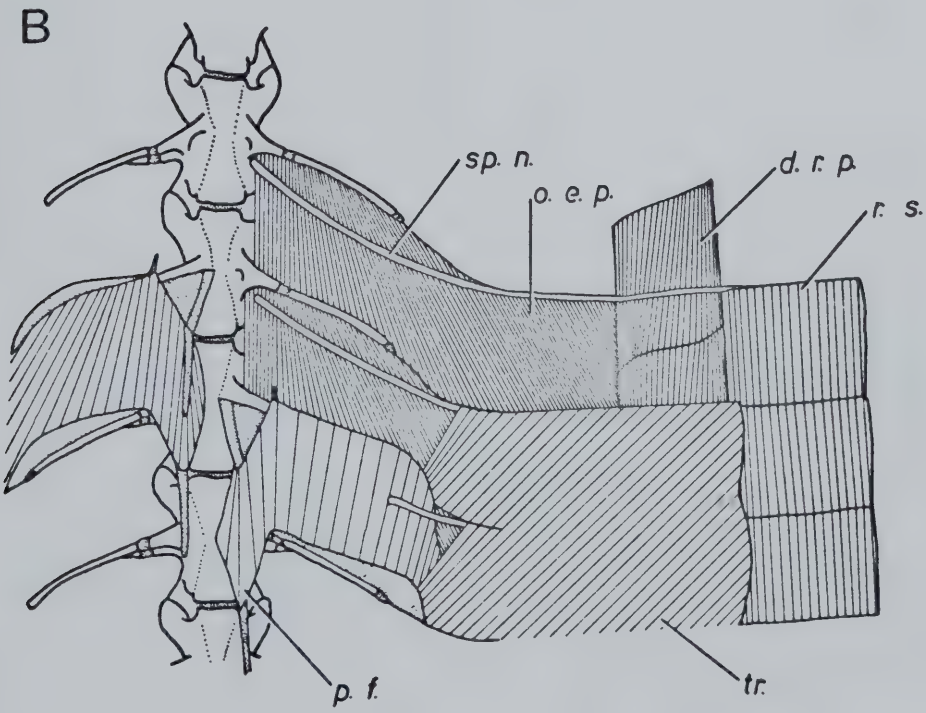
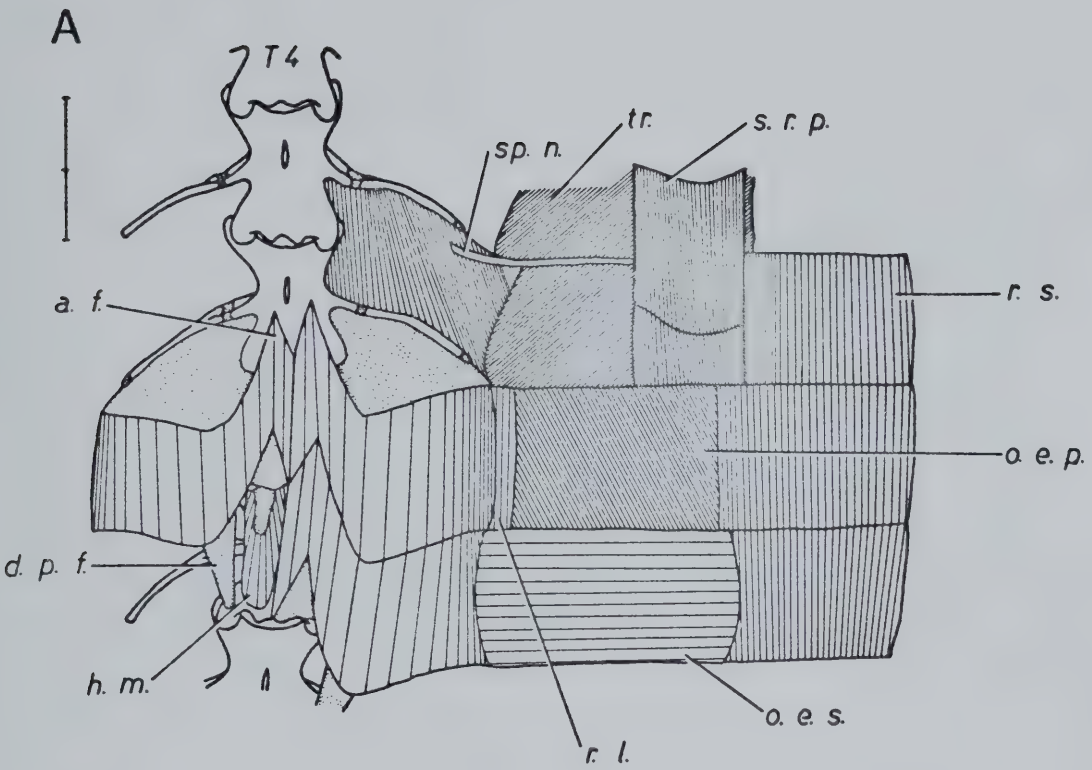


Figure 51. Dissection of *Plethodon vehiculum* with lateral abdominal musculature not shown complete: (A) dorsal view; (B) ventral view; scale represents two millimeters; abbreviations given on pp. 4-7.

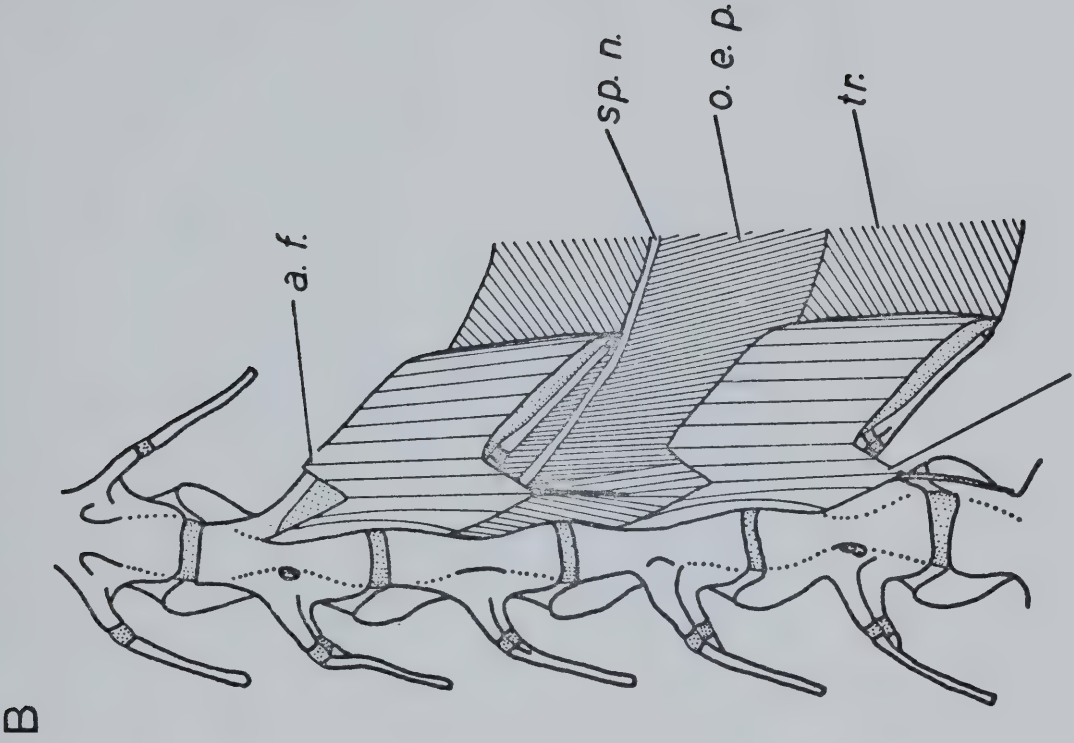
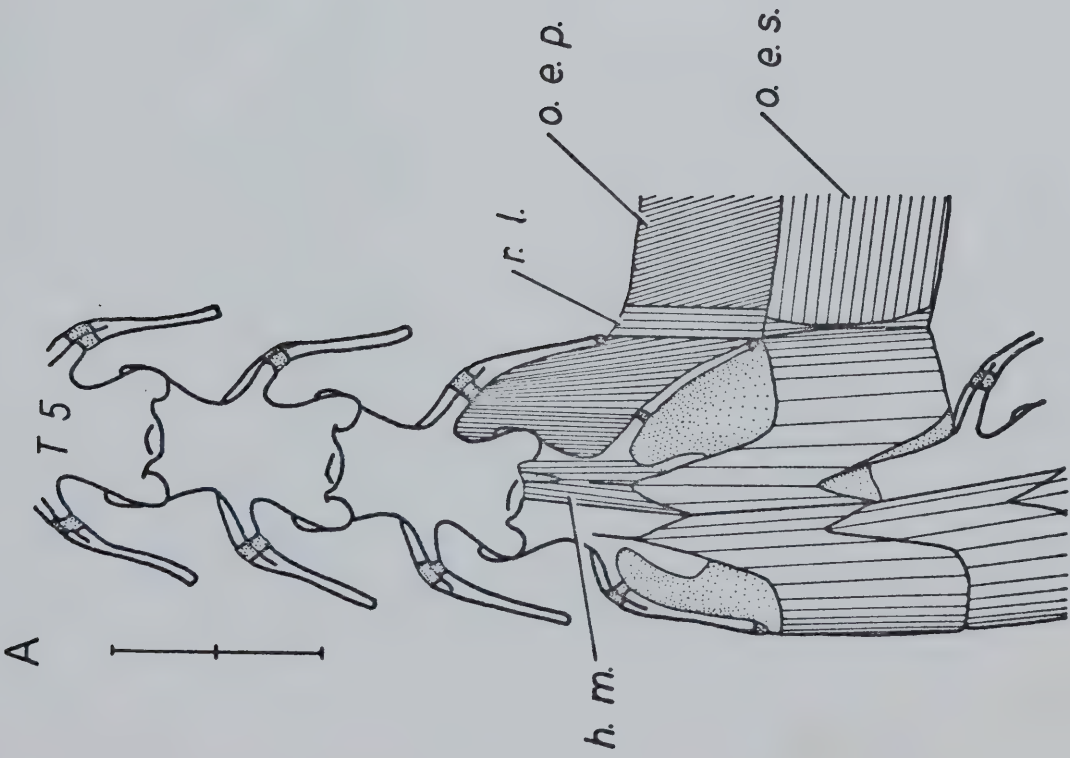


Figure 52. Dissection of *Plethodon neomexicanus* with lateral abdominal musculature spread laterally: (A) dorsal view; (B) ventral view; scale represents two millimeters; abbreviations given on pp. 4-7.

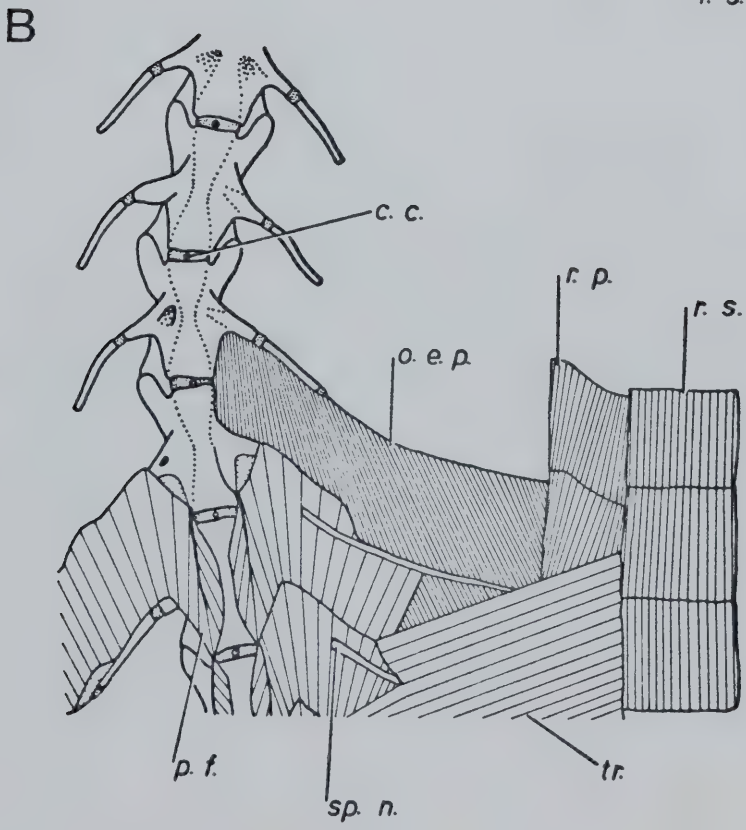
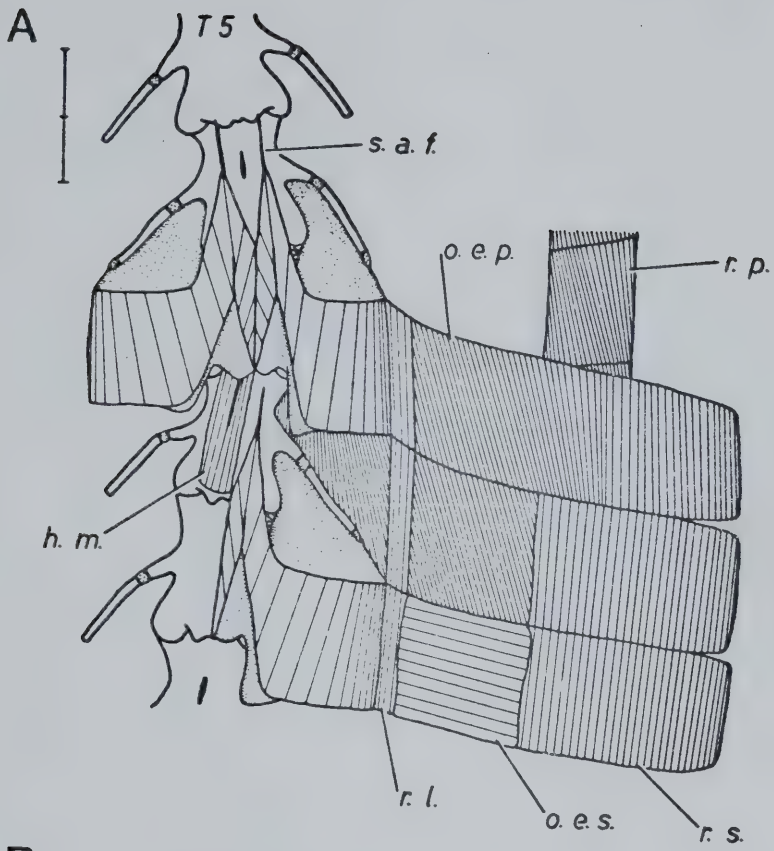


Figure 53. Dissection of young *Ensatina eschscholtzii* (snout-vent length ca. 30 mm) with lateral abdominal musculature spread laterally: (A) dorsal view; (B) ventral view; scale represents two millimeters; abbreviations given on pp. 4-7.

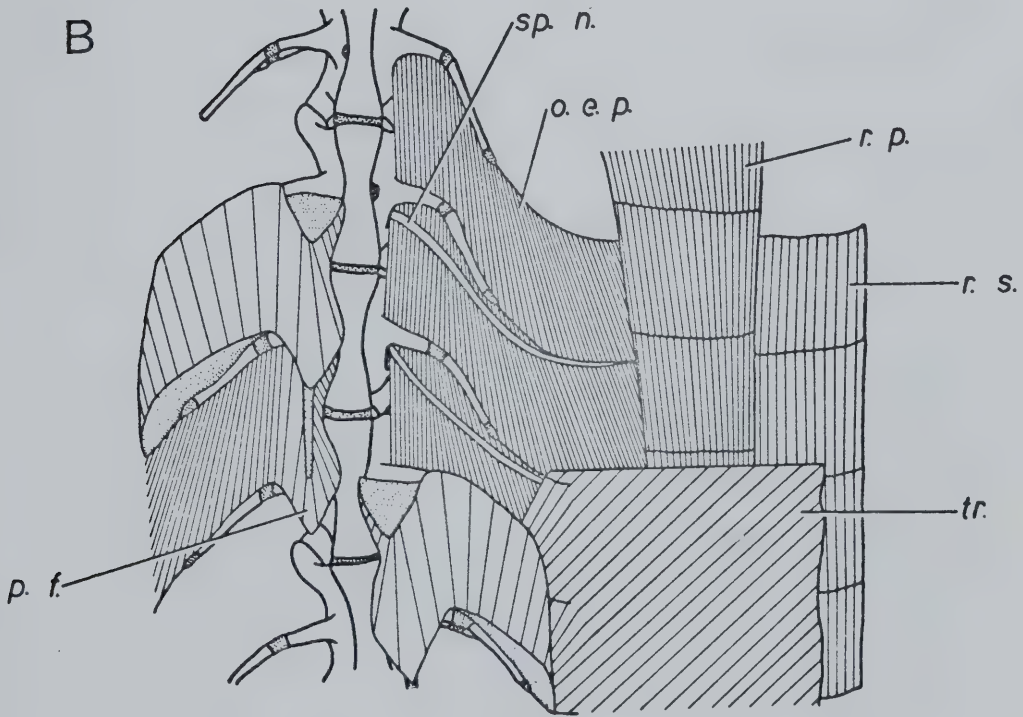
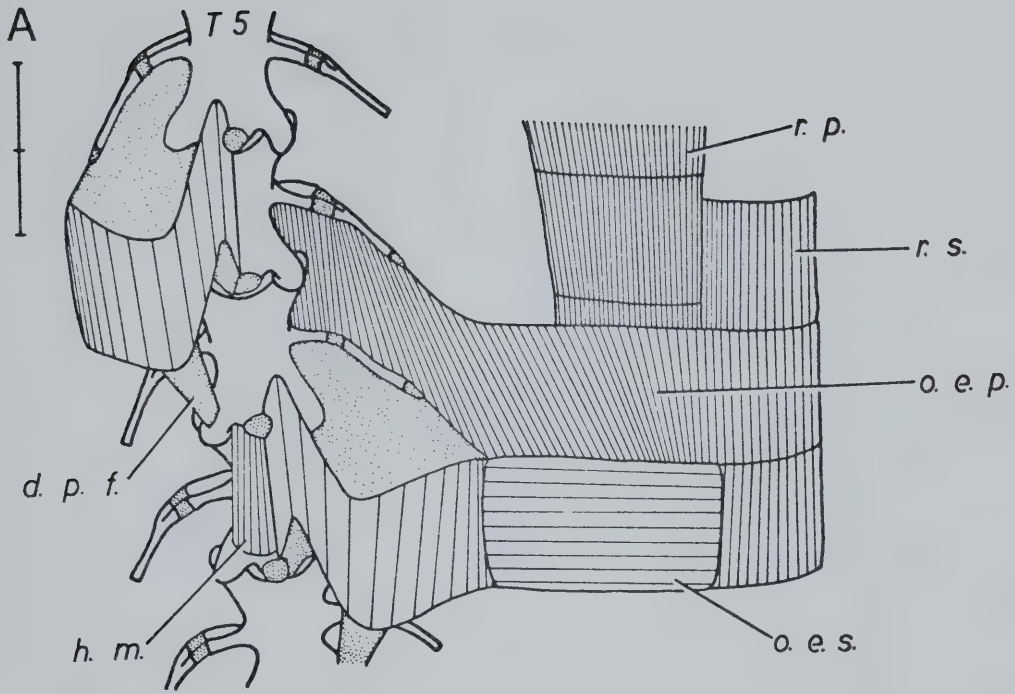


Figure 54. Dissection of large adult *Ensatina eschscholtzii*
with lateral abdominal musculature spread laterally;
(A) dorsal view; (B) ventral view; scale represents
two millimeters; abbreviations given on pp. 4-7.



Figure 55. Dissection of *Aneides lugubris* with lateral abdominal musculature spread laterally: (A) dorsal view; (B) ventral view; scale represents two millimeters; abbreviations given on pp. 4-7.

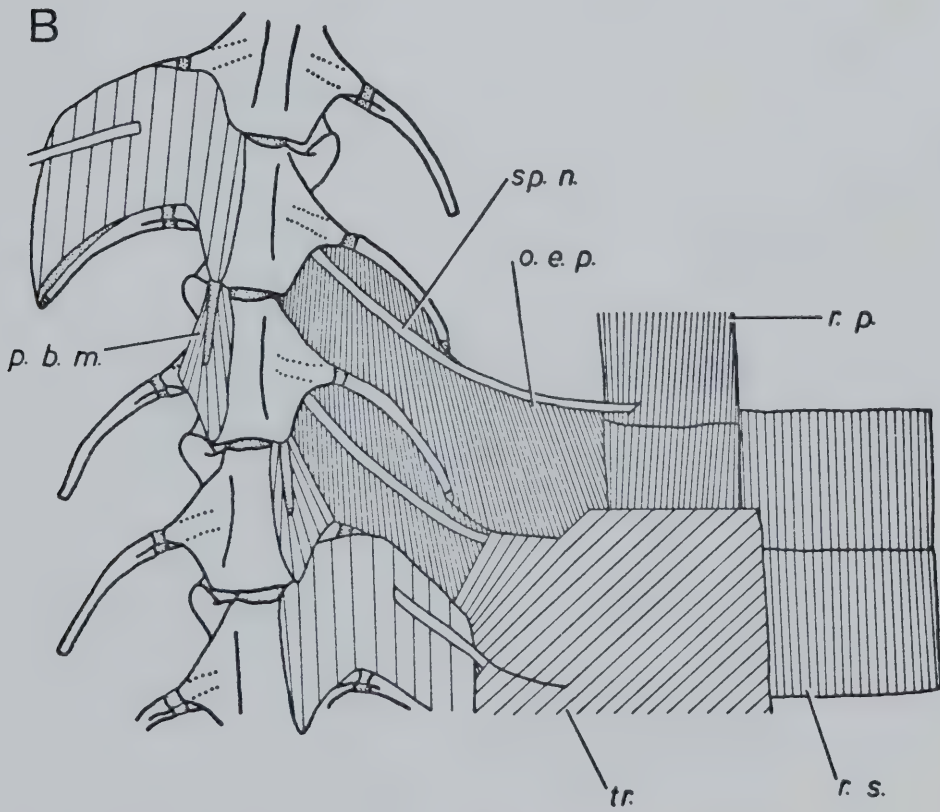
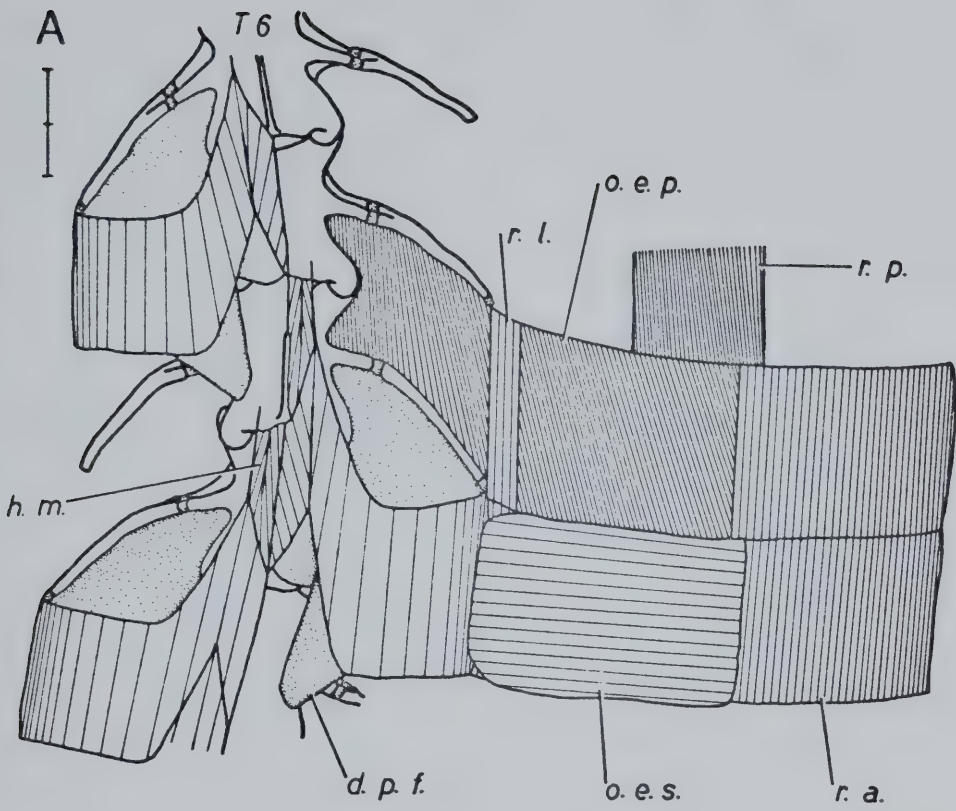


Figure 56. Dissection of *Hemidactylium scutatum* with lateral abdominal musculature spread laterally: (A) dorsal view; (B) ventral view; scale represents one millimeter; abbreviations given on pp. 4-7.

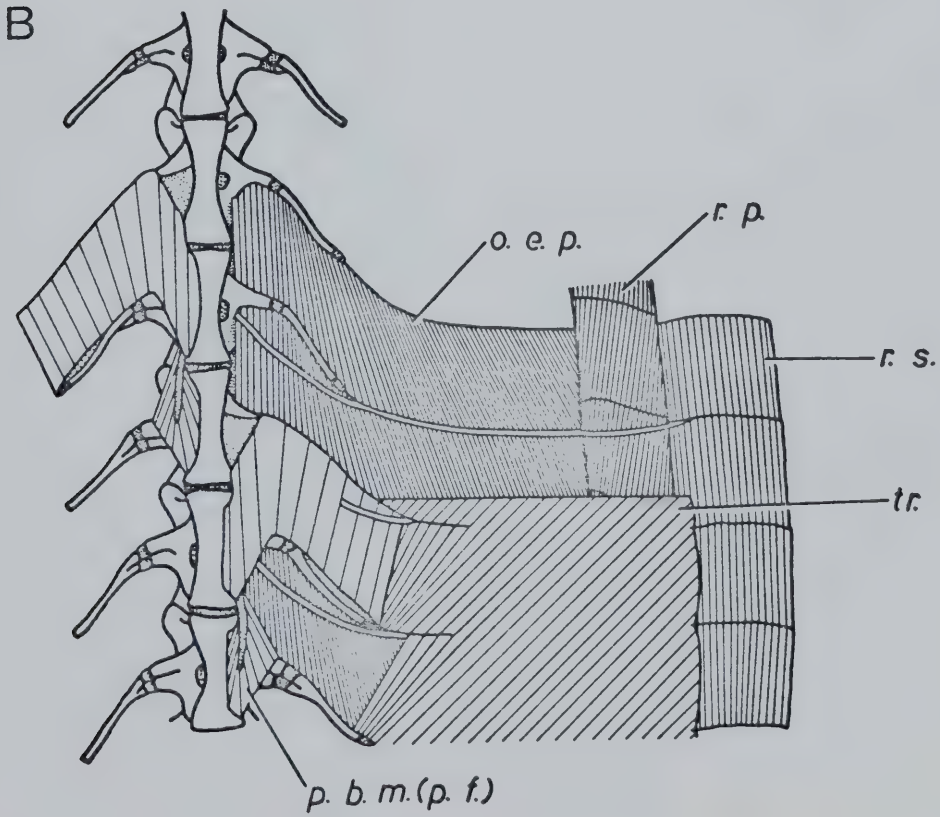
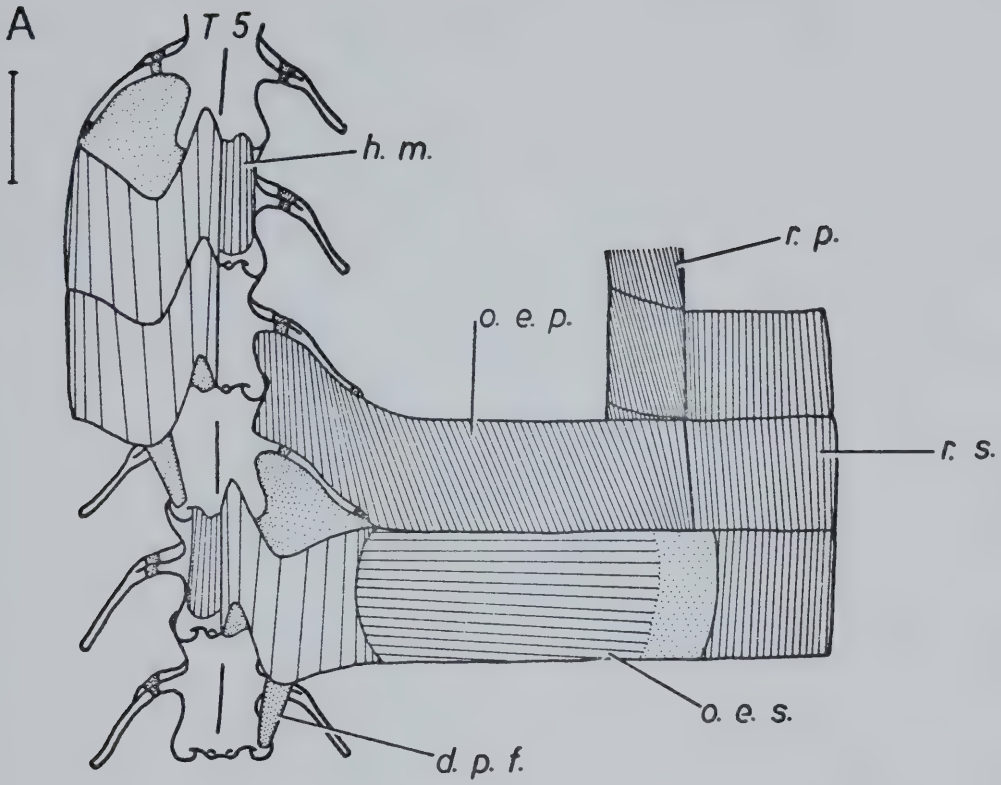


Figure 57. Dissection of *Batrachoseps attenuatus* with lateral abdominal musculature spread laterally: (A) dorsal view; (B) ventral view; scale represents two millimeters; abbreviations given on pp. 4-7.

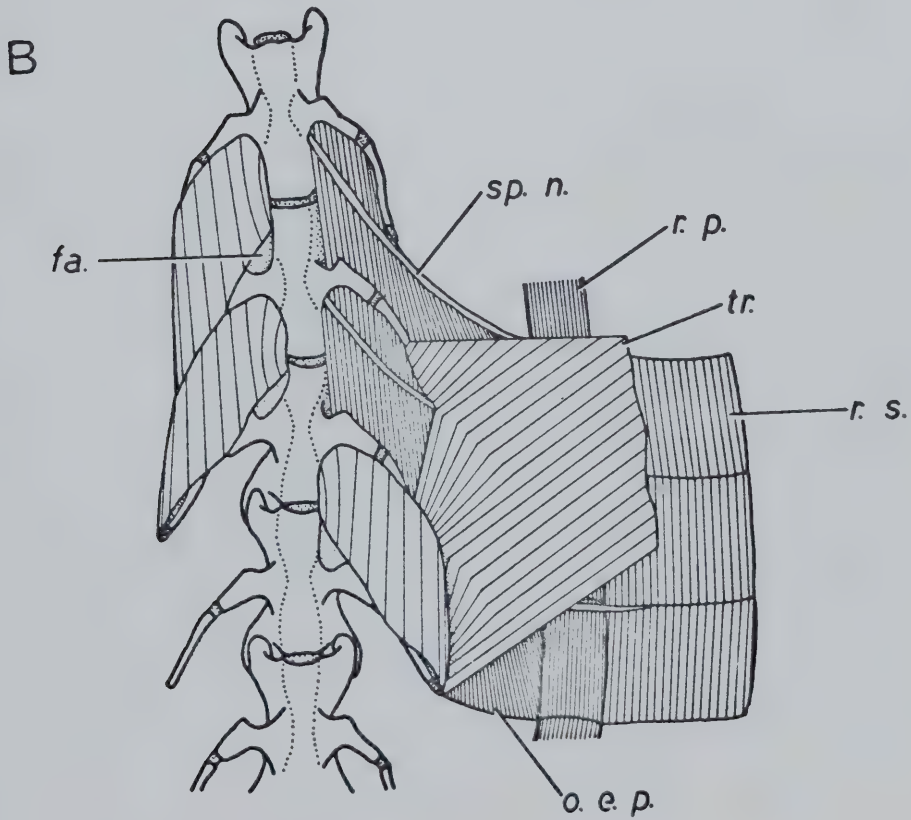
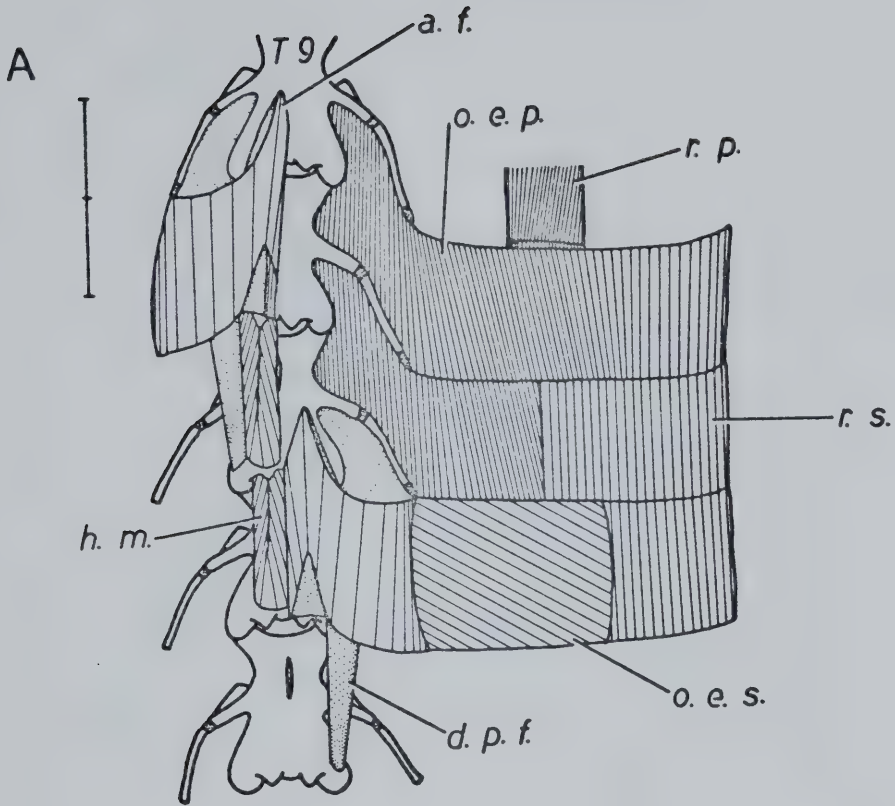


Figure 58. Dissection of *Bolitoglossa subpalmata* with lateral abdominal musculature spread laterally: (A) dorsal view; (B) ventral view; scale represents two millimeters; abbreviations given on pp. 4-7.

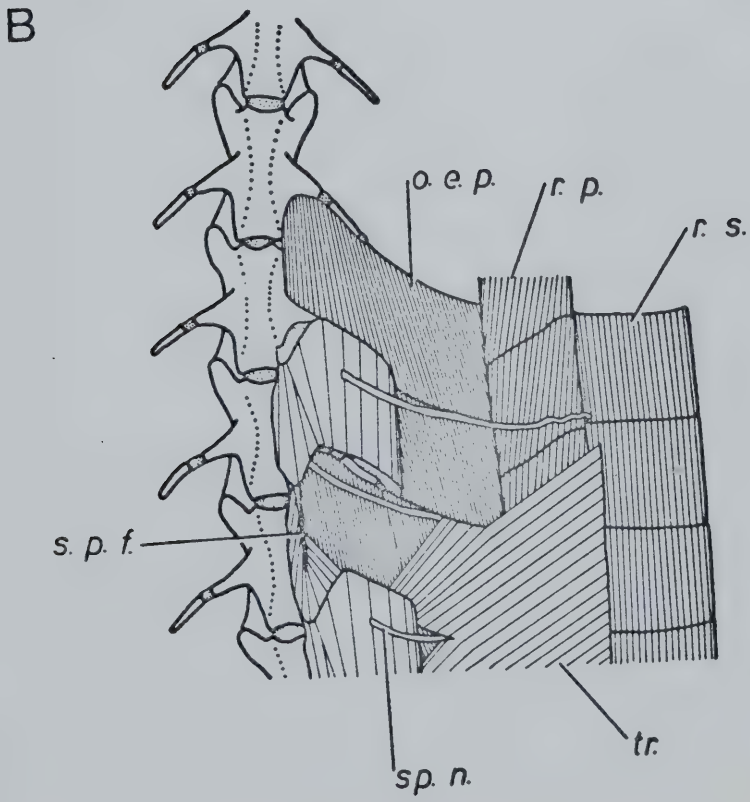
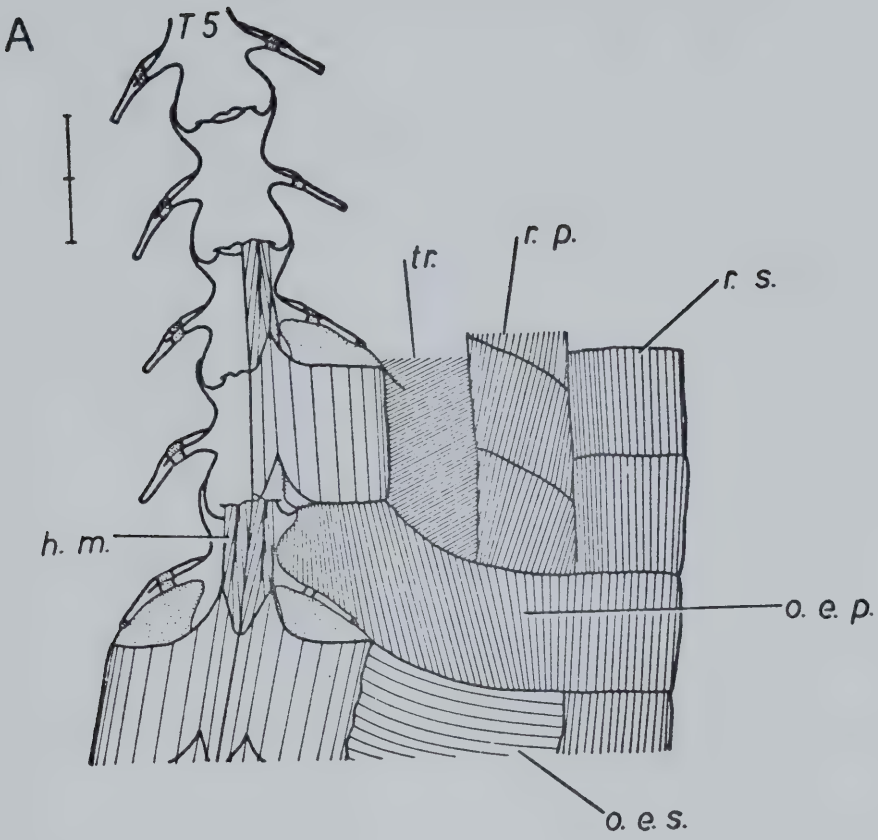


Figure 59. Dissection of *Pseudoeurycea cephalica* with lateral abdominal musculature spread laterally: (A) dorsal view; (B) ventral view; scale represents two millimeters; abbreviations given on pp. 4-7.

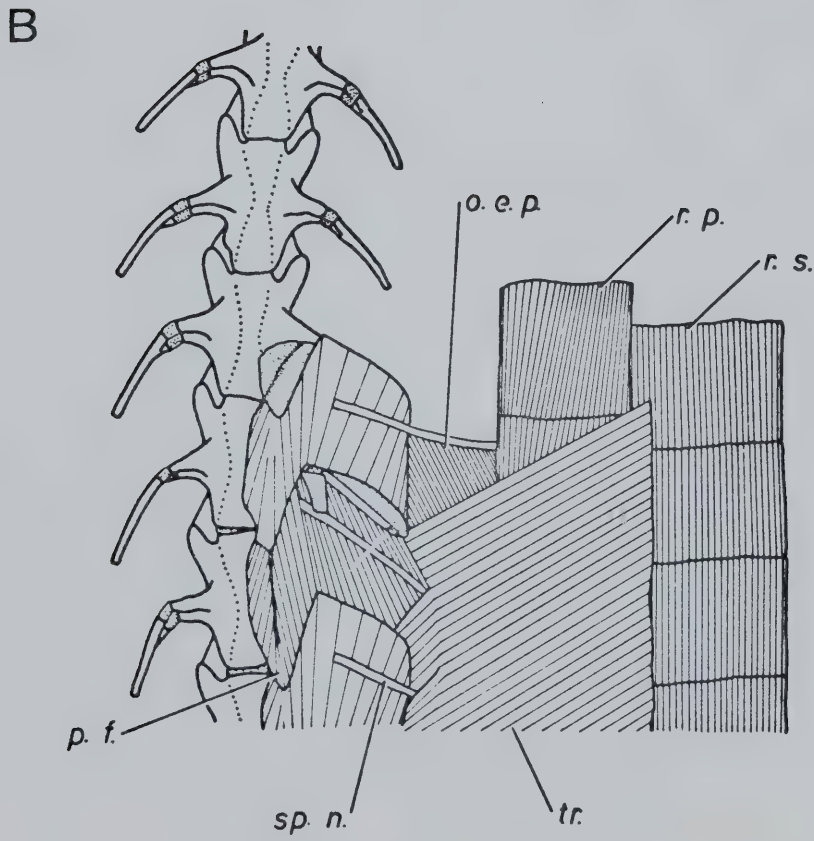
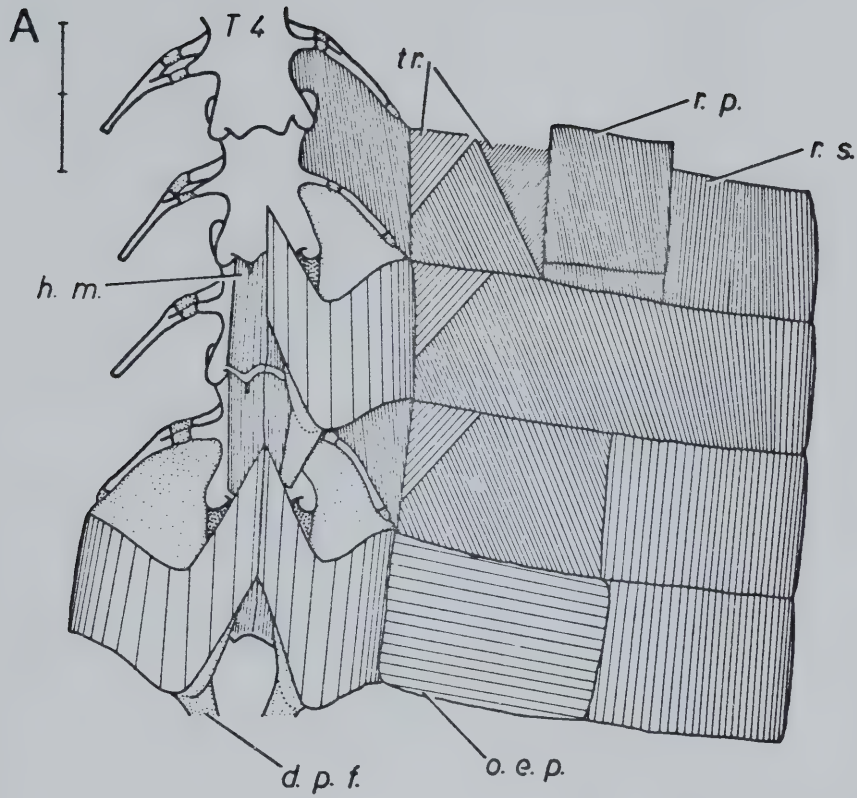


Figure 60. Dissection of *Chiropterotriton chiroptera* with lateral abdominal musculature spread laterally: (A) dorsal view; (B) ventral view; scale represents two millimeters; abbreviations given on pp. 4-7.

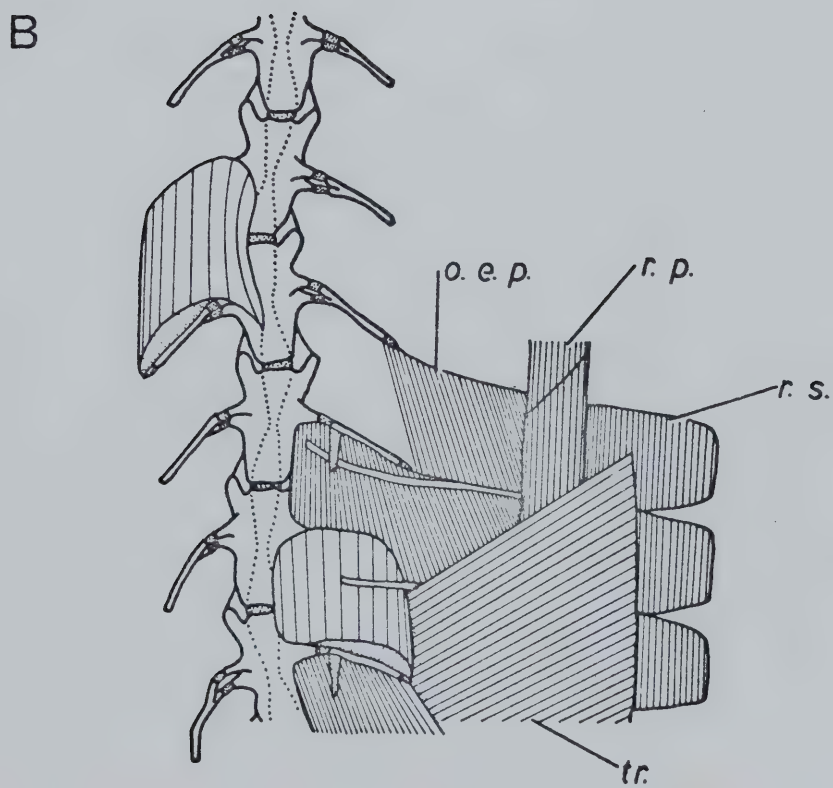
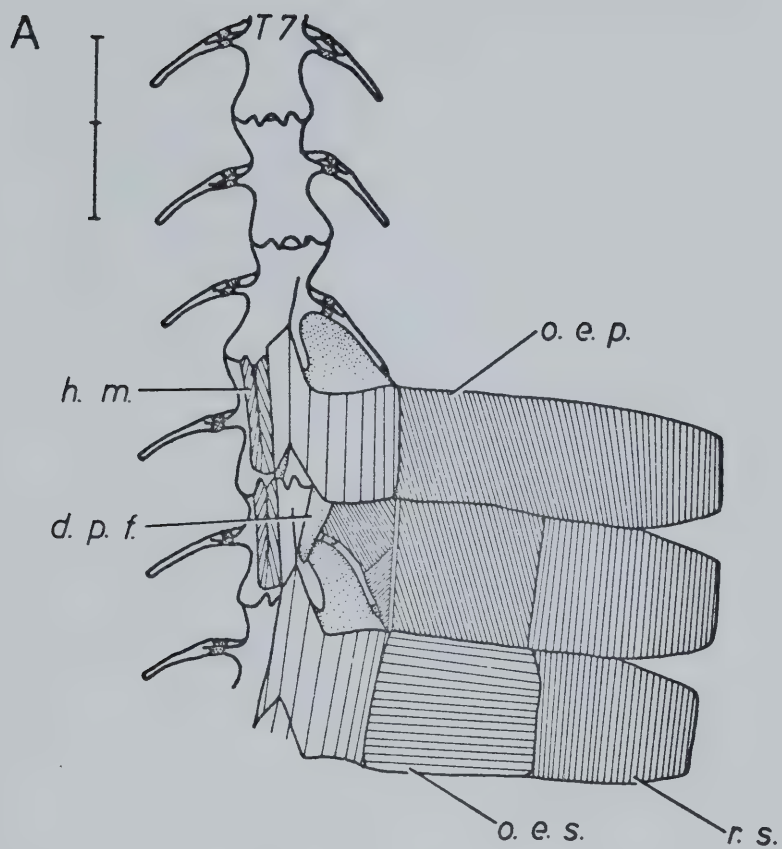


Figure 61. Dissection of *Eurycea bislineata* with lateral abdominal musculature spread laterally: (A) dorsal view; (B) ventral view; scale represents one millimeter; abbreviations given on pp. 4-7.

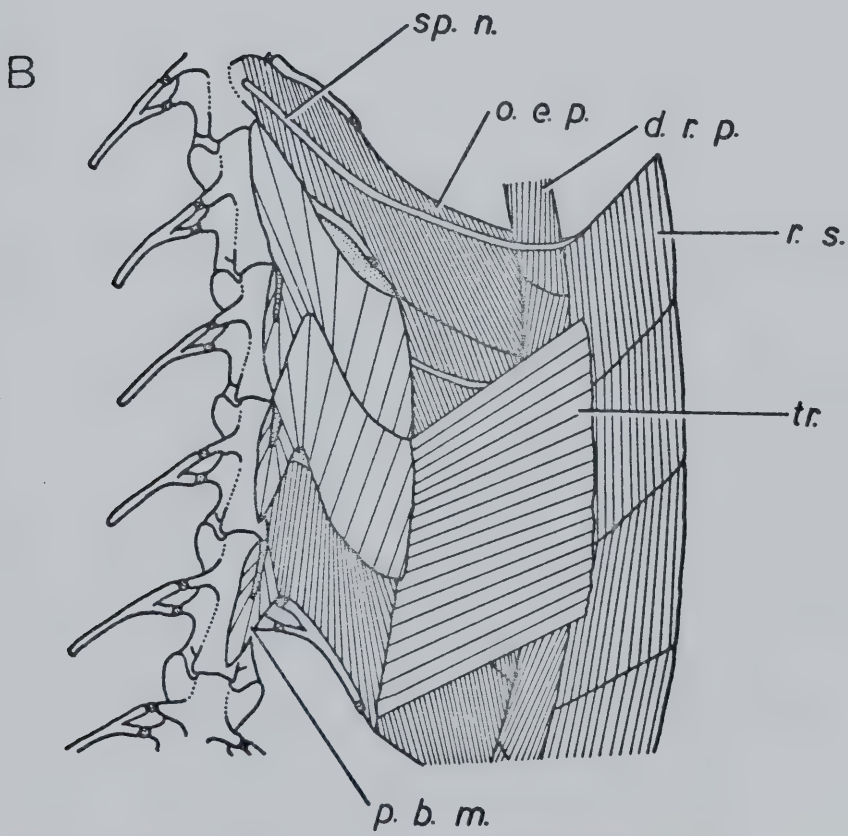
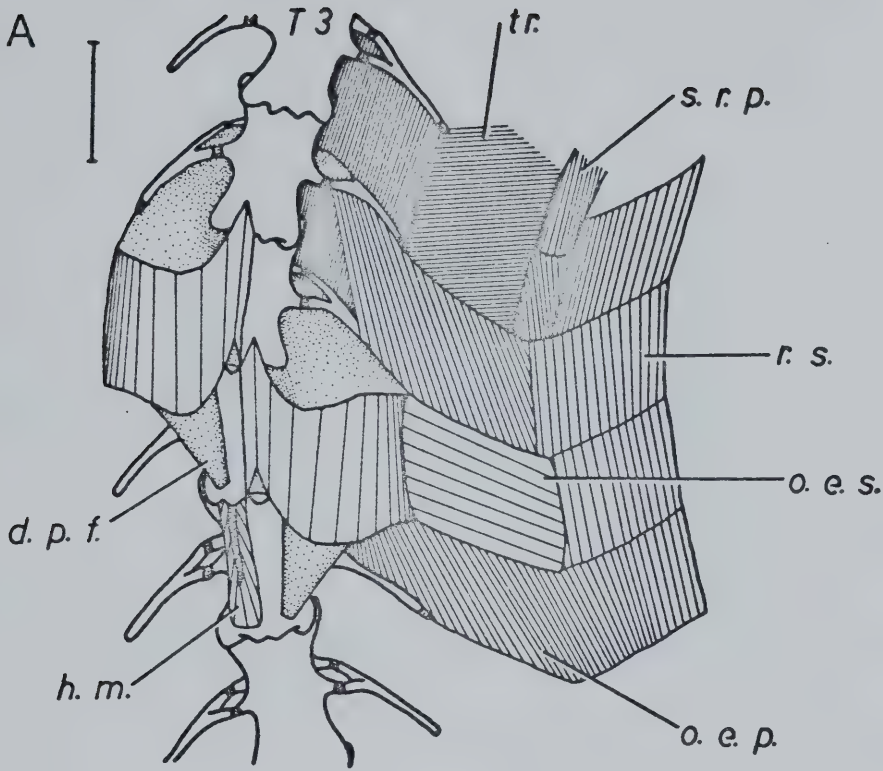


Figure 62. Dissection of *Eurycea quadridigitata* with lateral abdominal musculature spread laterally: (A) dorsal view; (B) ventral view; scale represents one millimeter; abbreviations given on pp. 4-7.

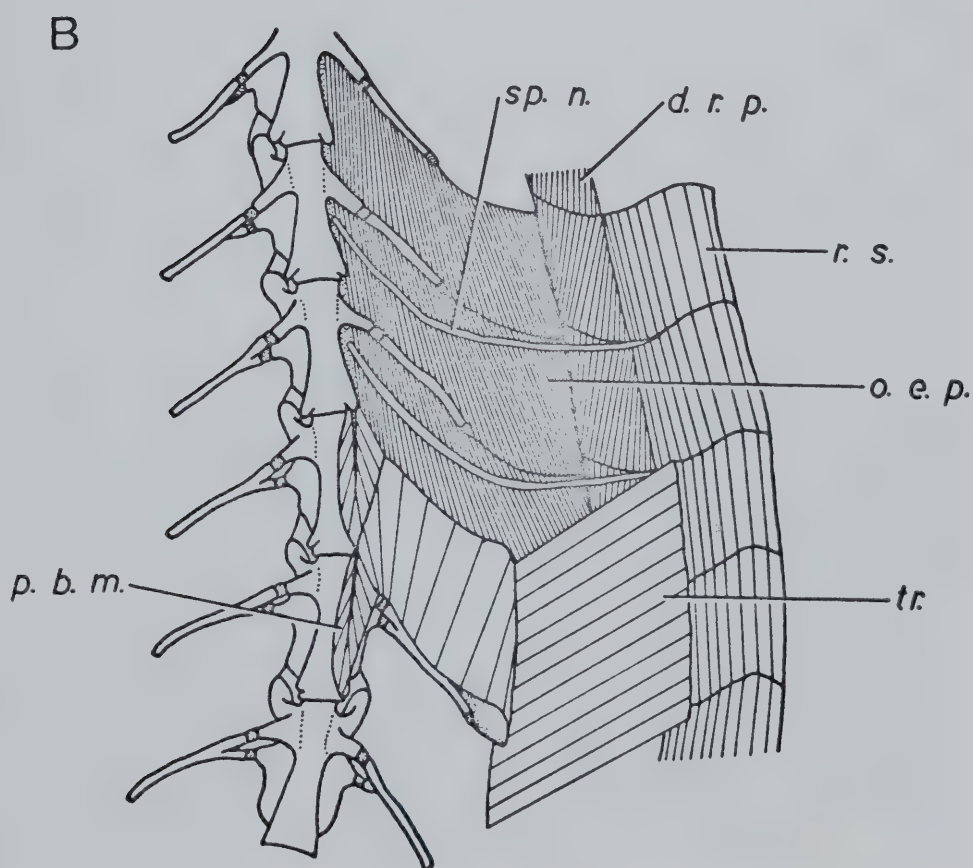
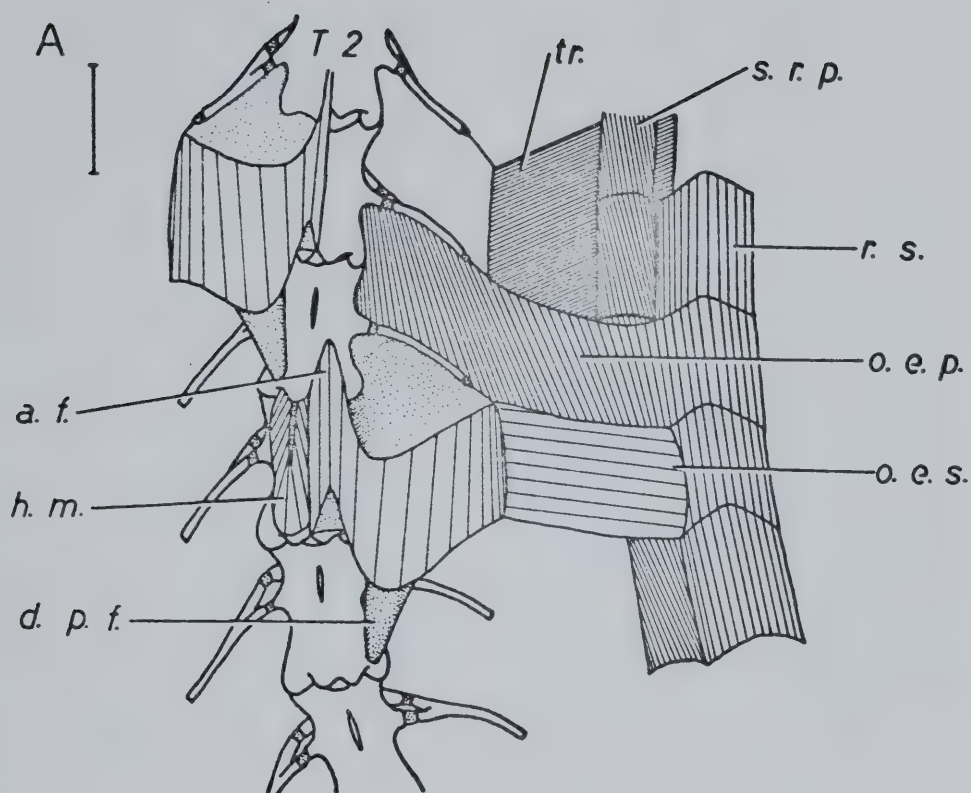


Figure 63. Dissection of *Typhlotriton spelaeus* with lateral abdominal musculature spread laterally: (A) dorsal view; (B) ventral view; scale represents two millimeters; abbreviations given on pp. 4-7.

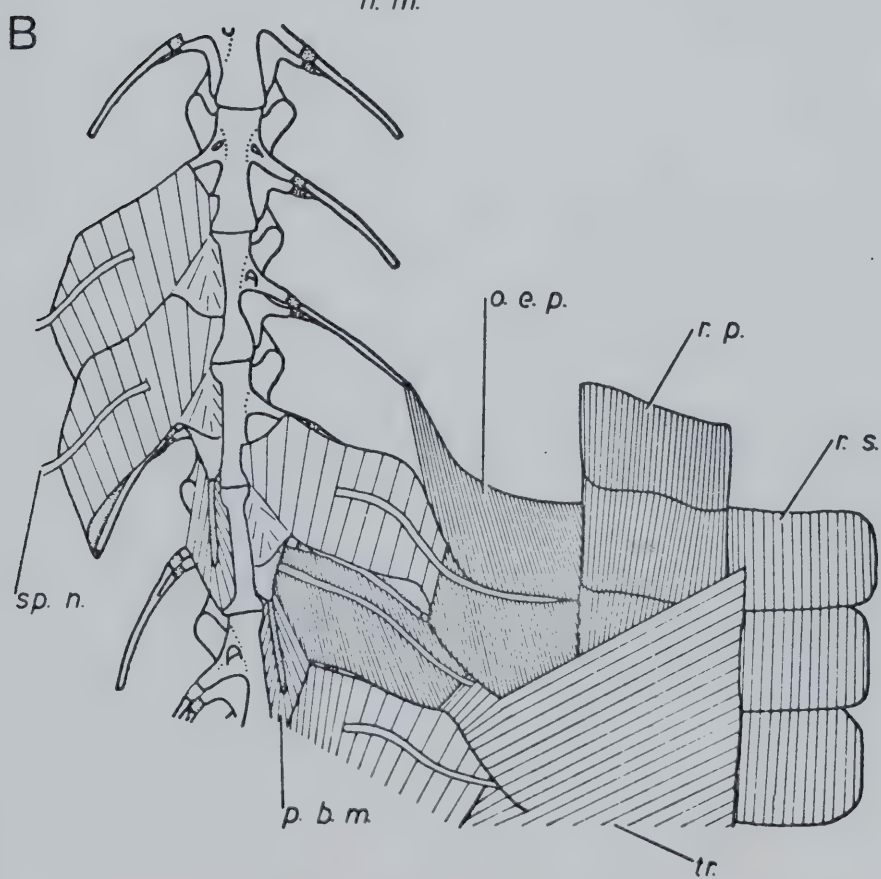
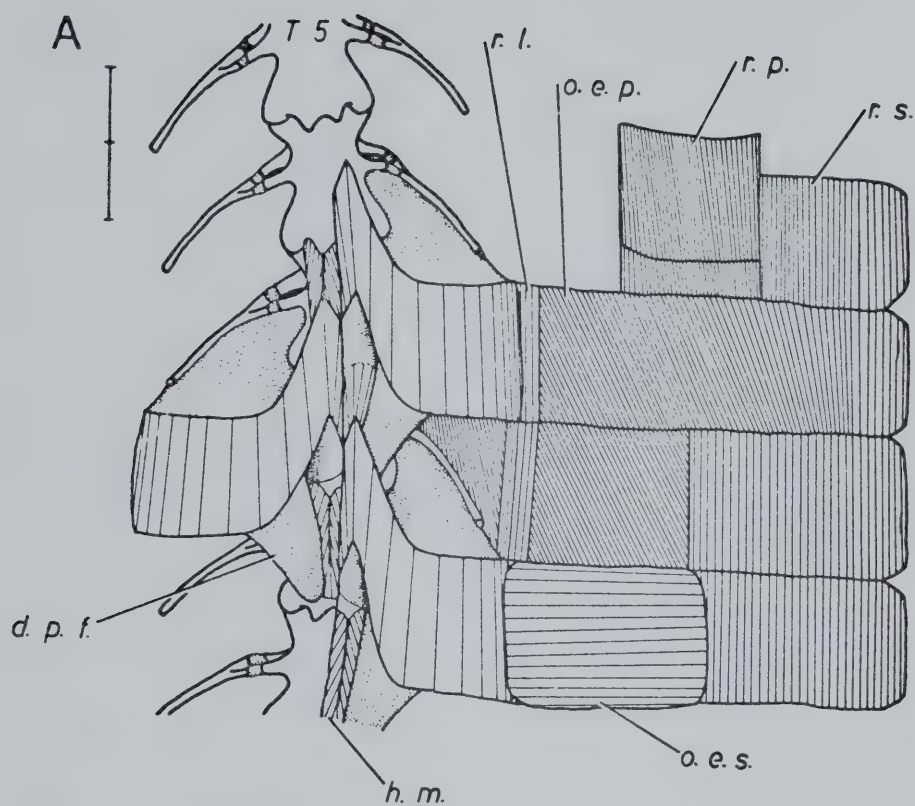


Figure 64. Dissection of *Stereochilus marginatus* with lateral abdominal musculature spread laterally: (A) dorsal view; (B) ventral view; scale represents two millimeters; abbreviations given on pp. 4-7.

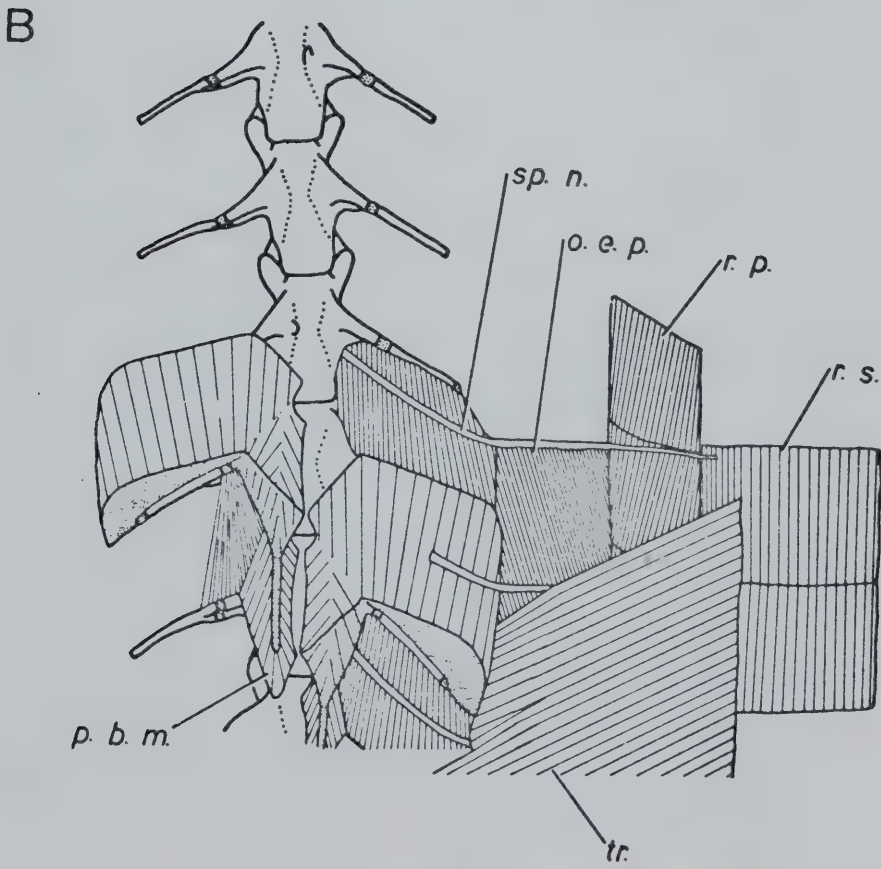
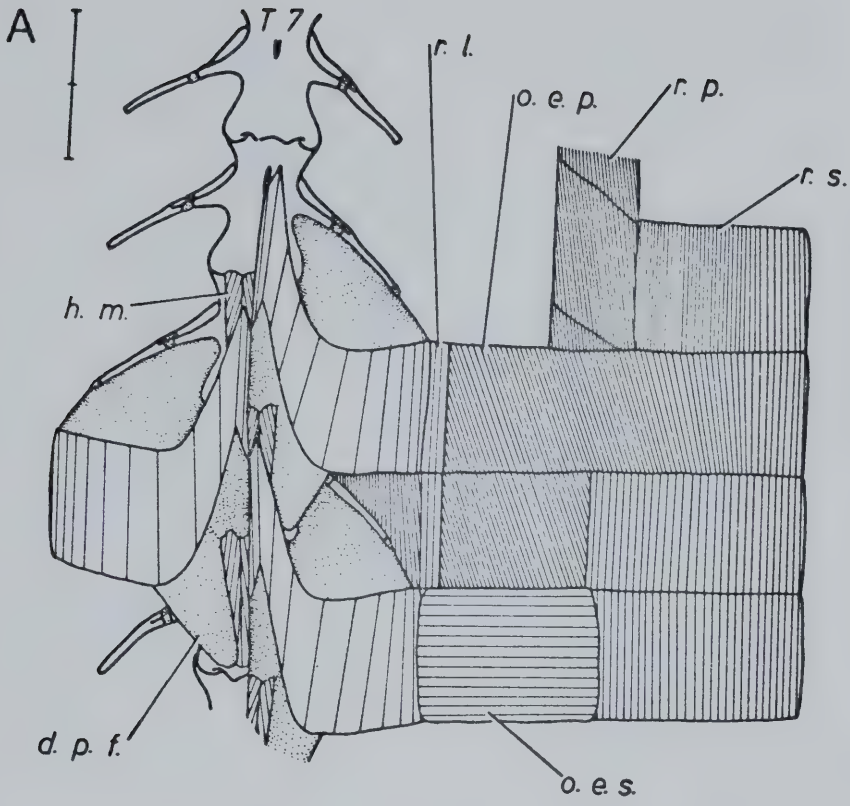


Figure 65. Dissection of *Gyrinophilus porphyriticus* with lateral abdominal musculature spread laterally: (A) dorsal view, a small *rectus lateralis* is present but not figured; (B) ventral view; scale represents two millimeters; abbreviations given on pp. 4-7.

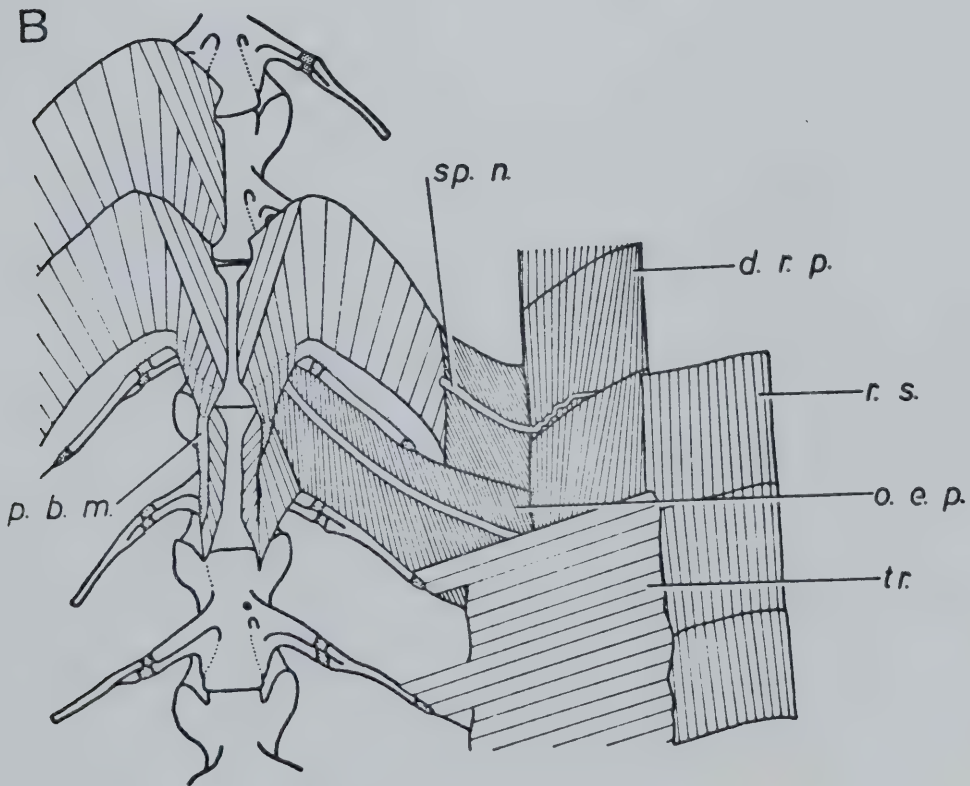
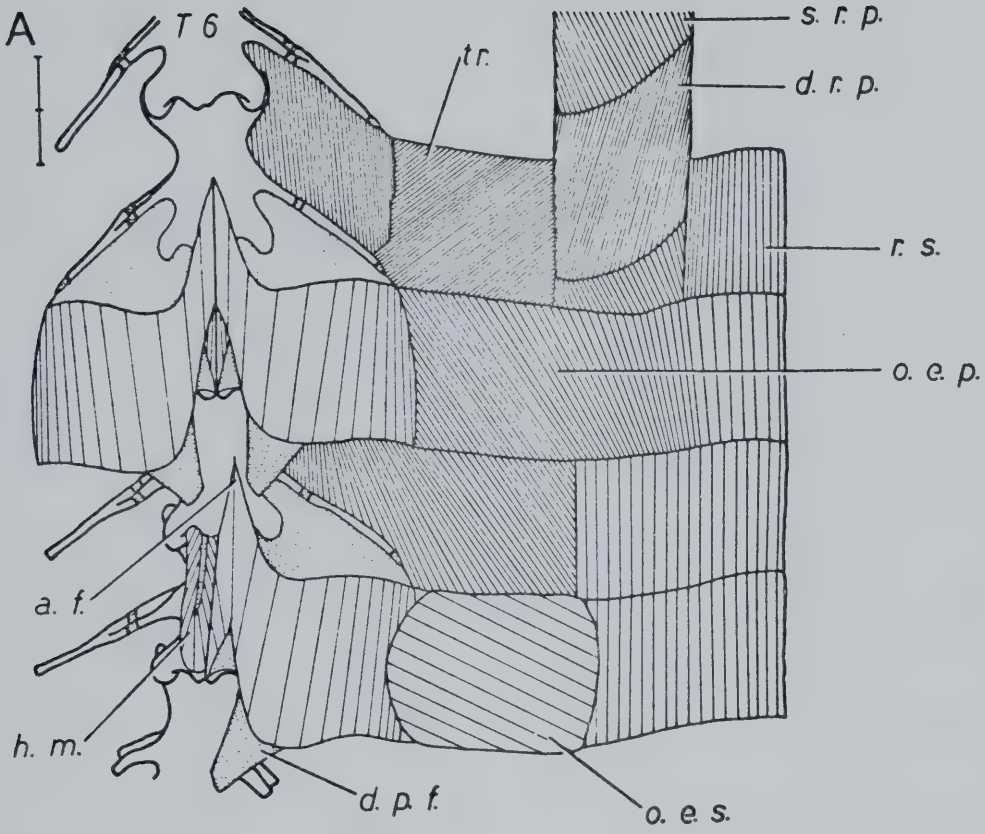


Figure 66. Dissection of *Pseudotriton ruber* with lateral abdominal musculature spread laterally: (A) dorsal view, a small, ill-defined *rectus lateralis* is present but not figured; (B) ventral view; scale represents two millimeters; abbreviations given on pp. 4-7.

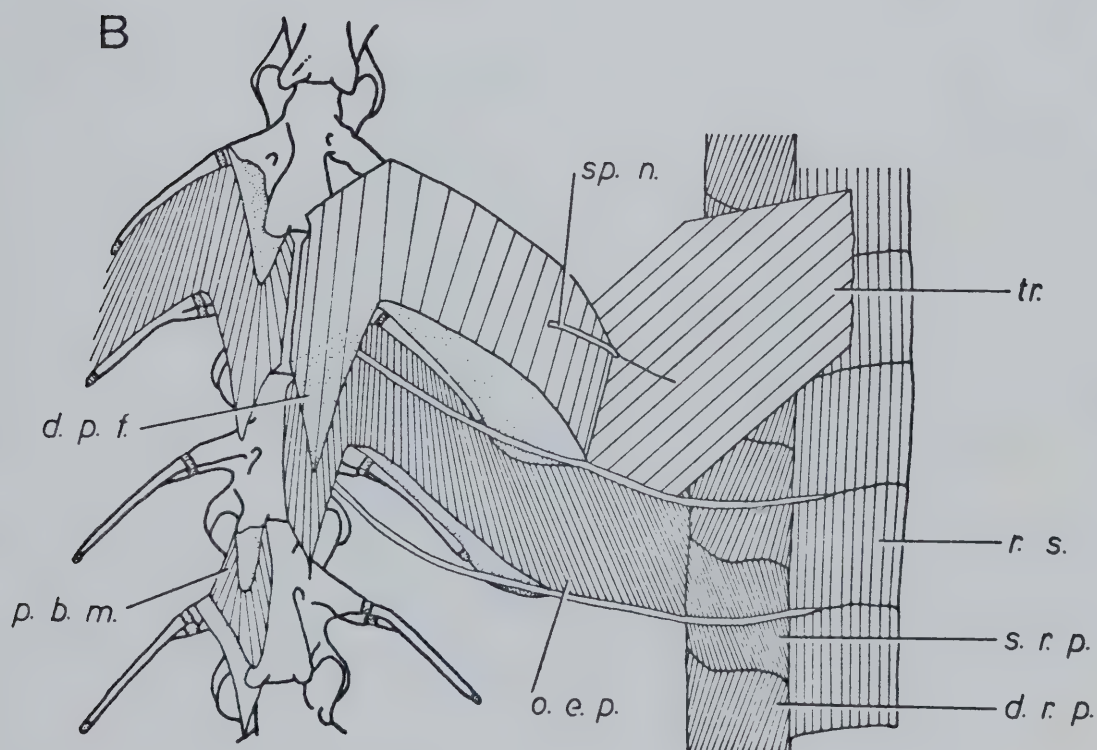
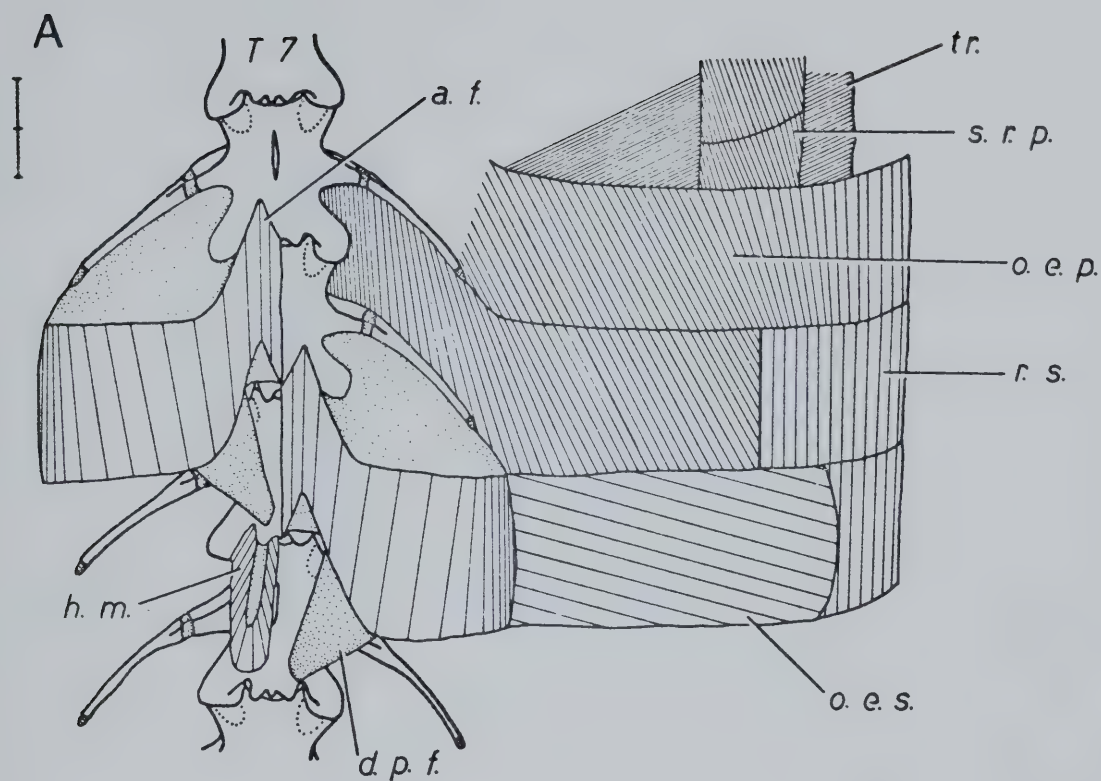


Figure 67. Dissection of *Desmognathus fuscus* with lateral abdominal musculature spread laterally: (A) dorsal view; (b) ventral view; scale represents two millimeters; abbreviations given on pp. 4-7.

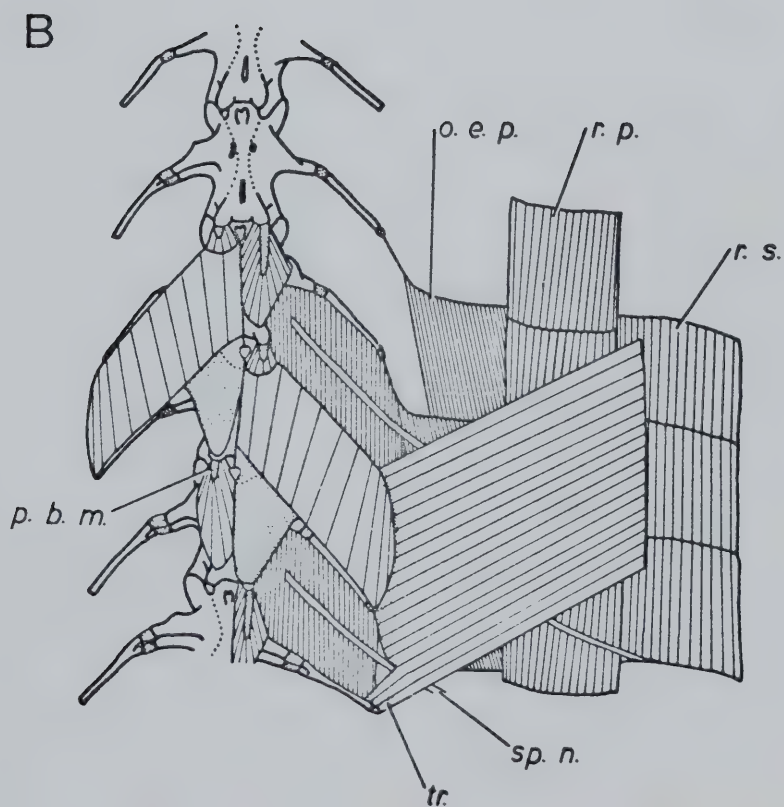
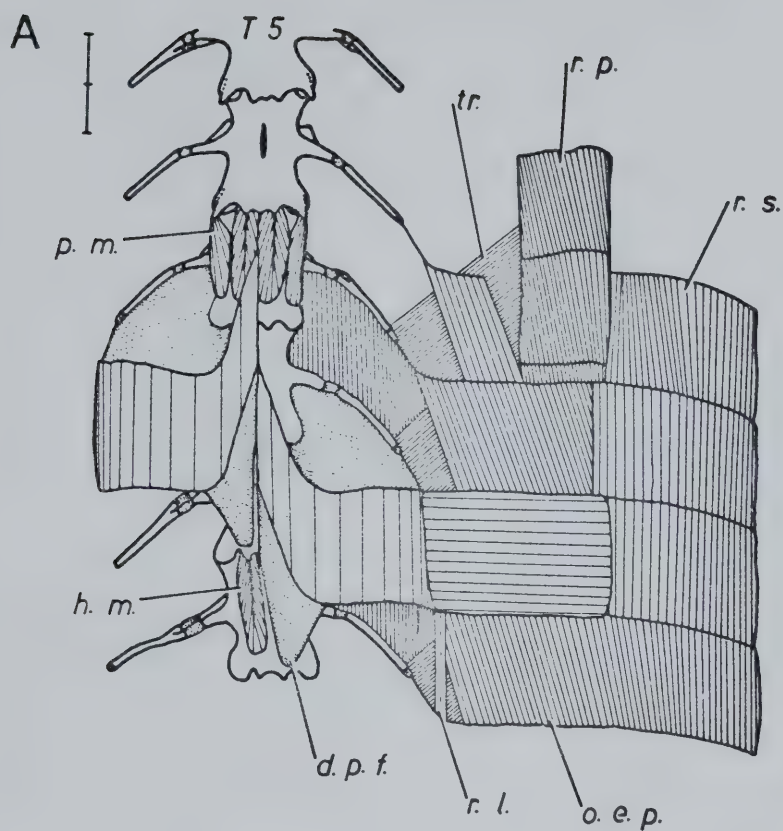


Figure 68. Dissection of *Leurognathus marmoratus* with lateral abdominal musculature spread laterally: (A) dorsal view; (B) ventral view; scale represents two millimeters; abbreviations given on pp. 4-7.

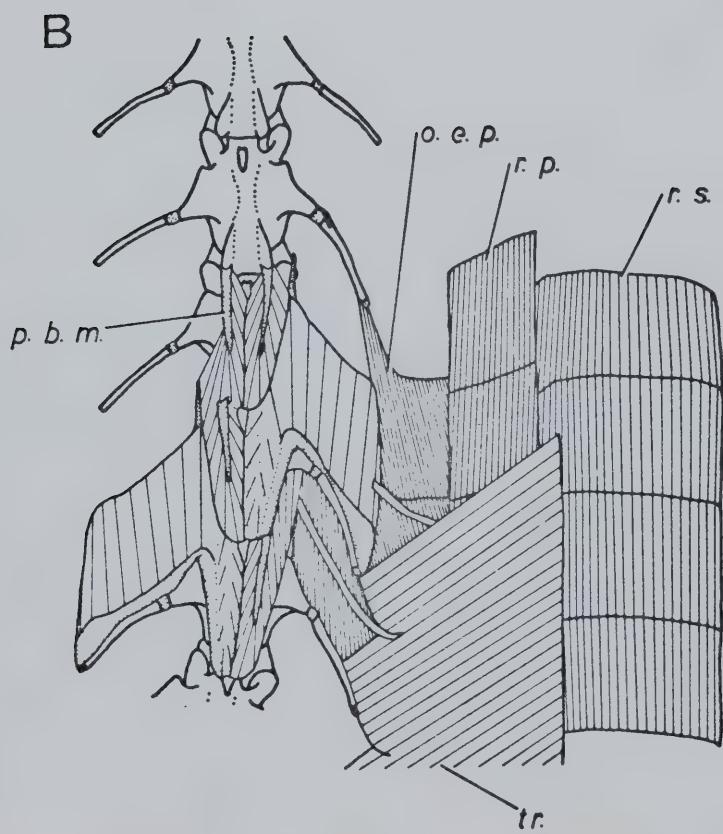
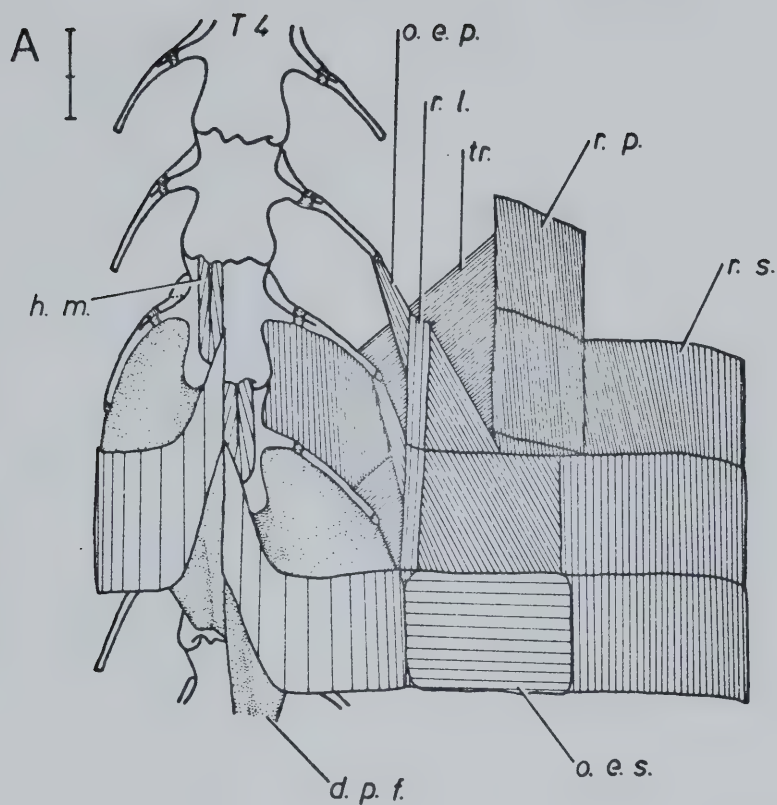


Figure 69. Dissection of *Salamandra salamandra* with lateral abdominal musculature spread laterally: (A) dorsal view, displacement of anterior flexures by the dorsal glands not shown; (B) ventral view; scale represents two millimeters; abbreviations given on pp. 4-7.

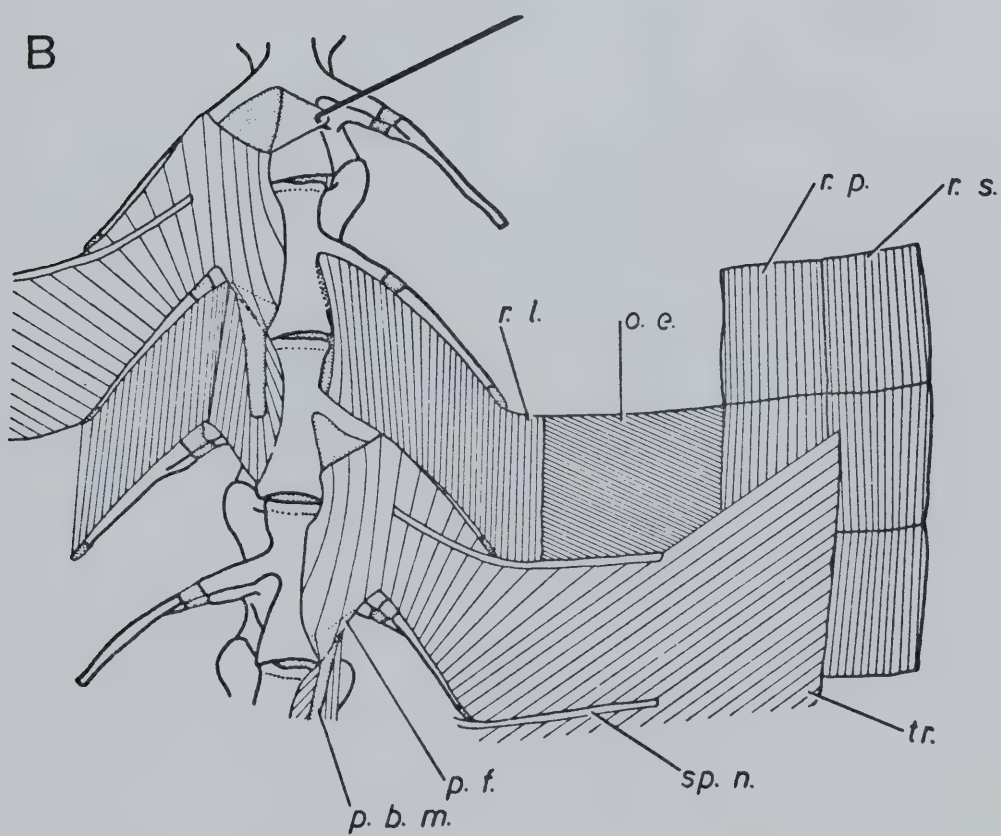
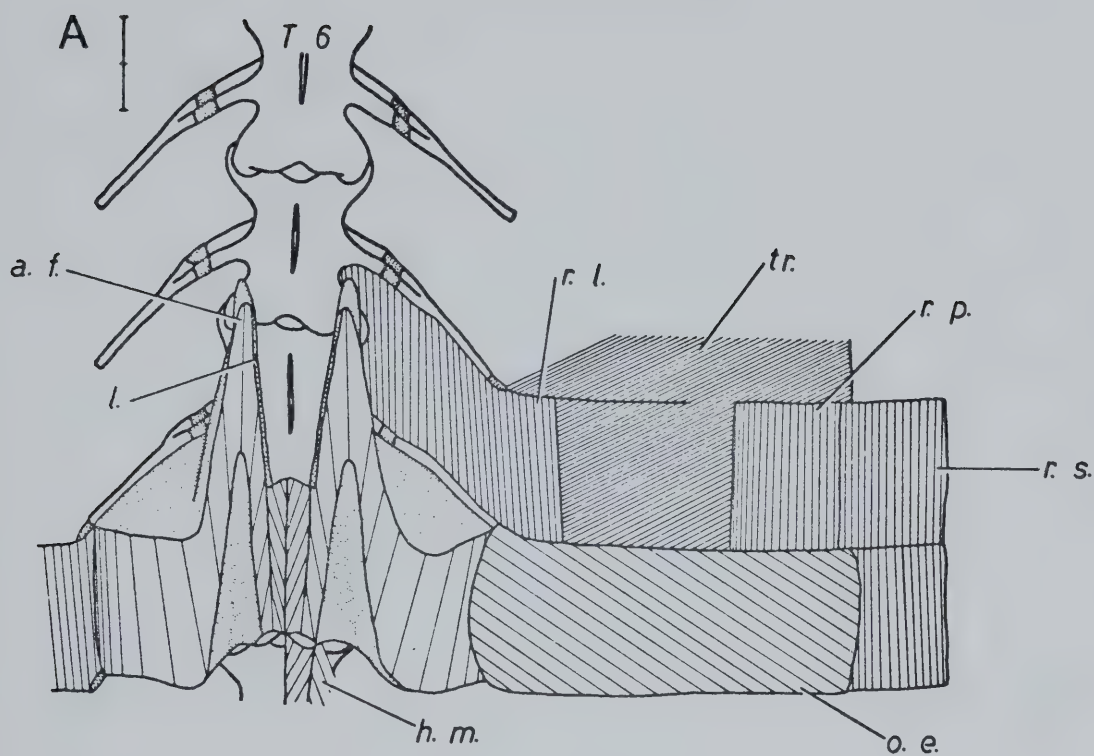


Figure 70. *Salamandra salamandra*: camera lucida sketch of vertebrae from the midtrunk of a juvenile to show the position of the paired poison glands with respect to the column.

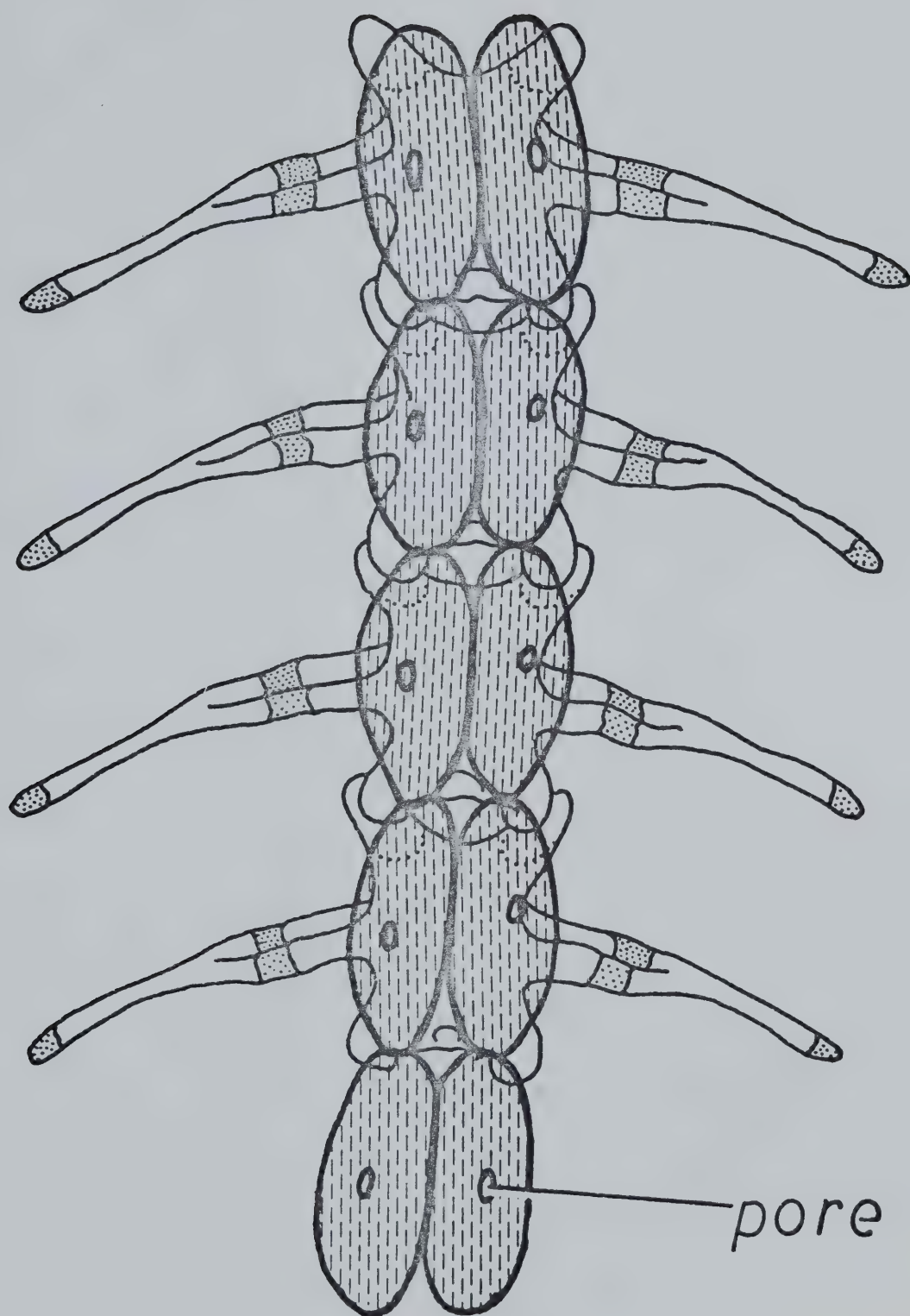


Figure 71. Dissection of *Pleurodeles waltli* with lateral abdominal musculature spread laterally: (A) dorsal view; (B) ventral view; scale represents two millimeters; abbreviations given on pp. 4-7.

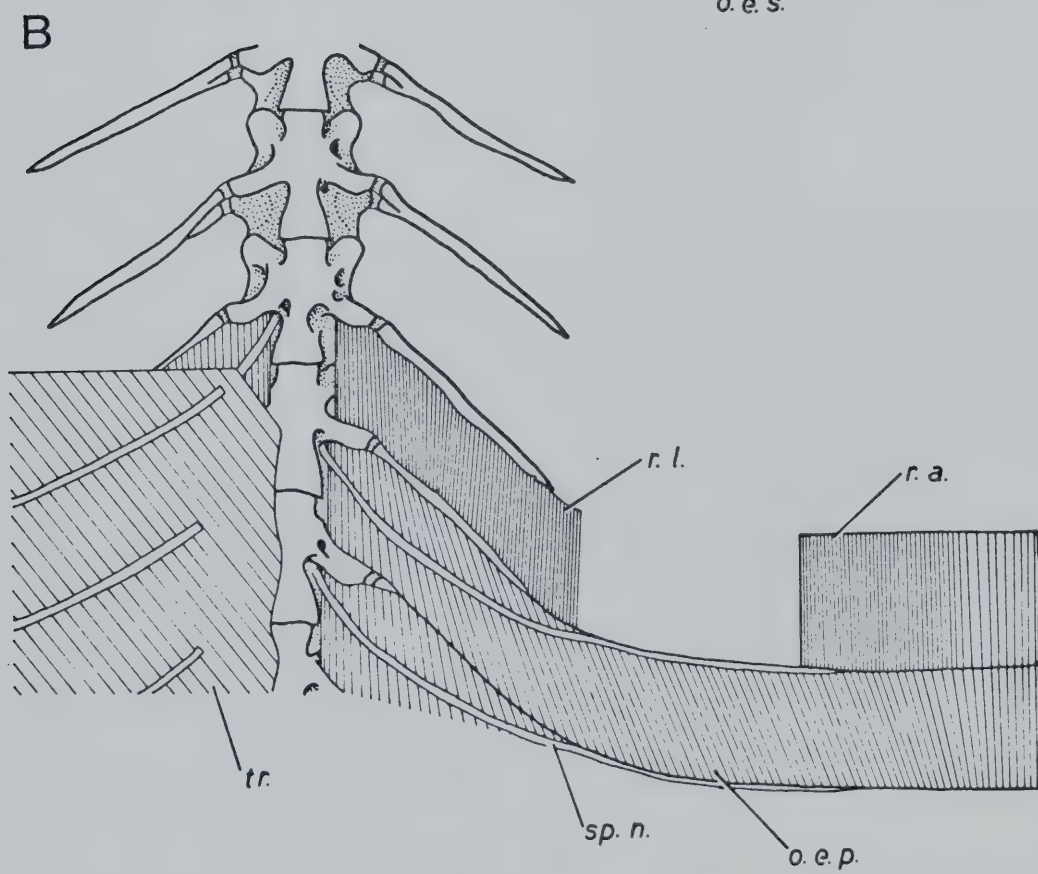
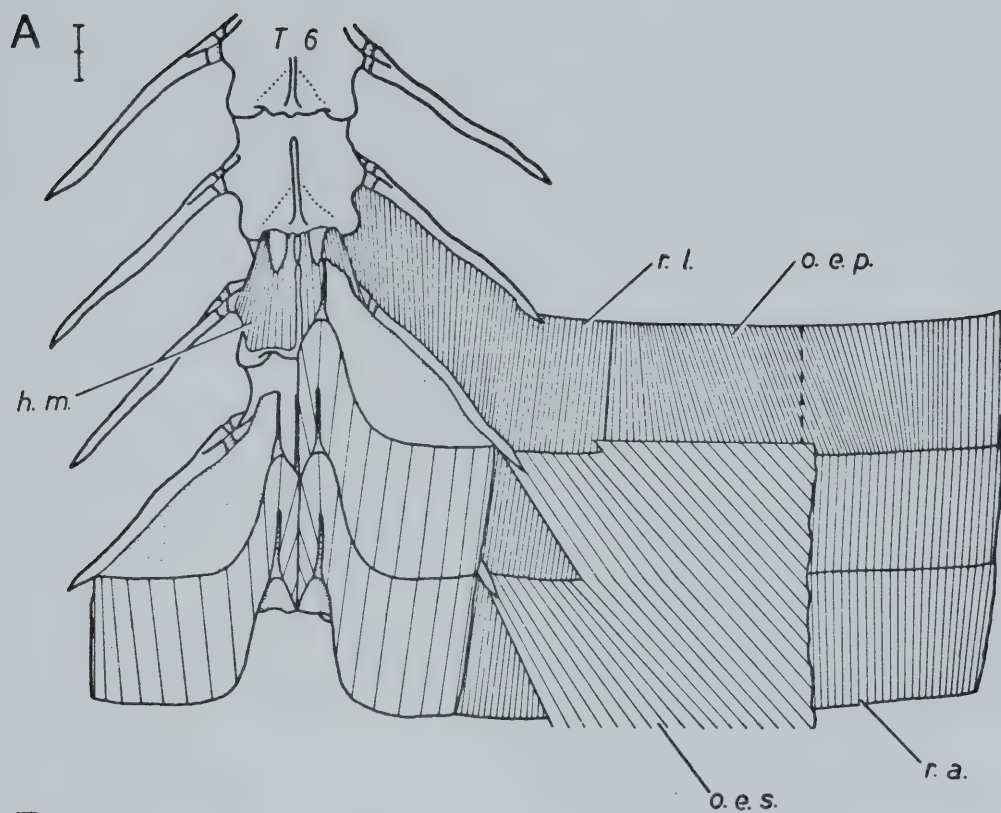


Figure 72. Dissection of *Salamandrina terdigitata* with lateral abdominal musculature spread laterally: (A) dorsal view; (B) ventral view; scale represents two millimeters; abbreviations given on pp. 4-7.

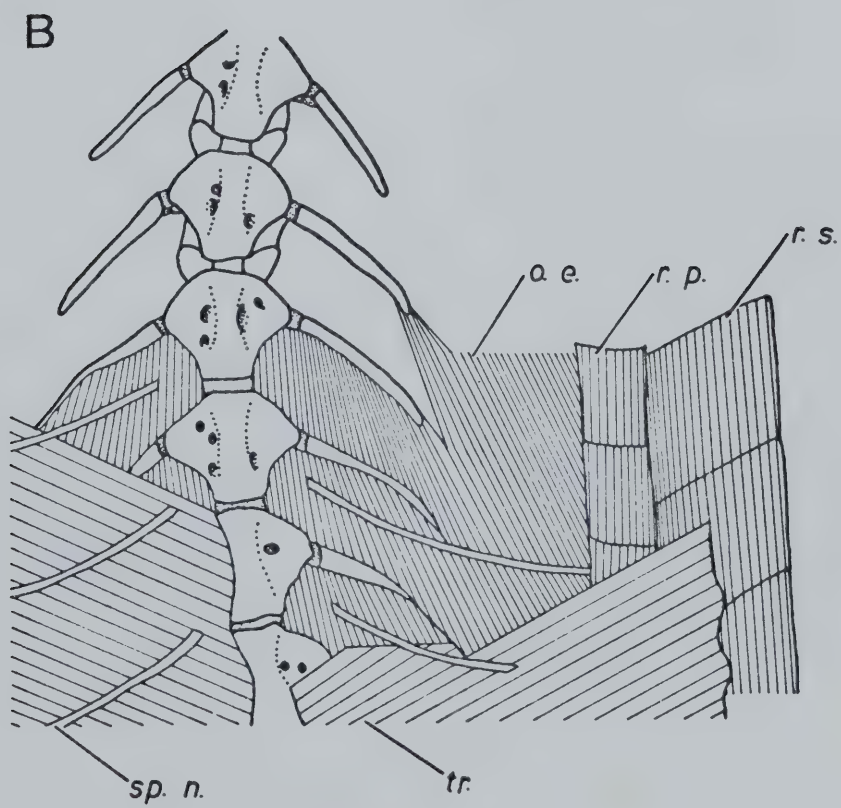
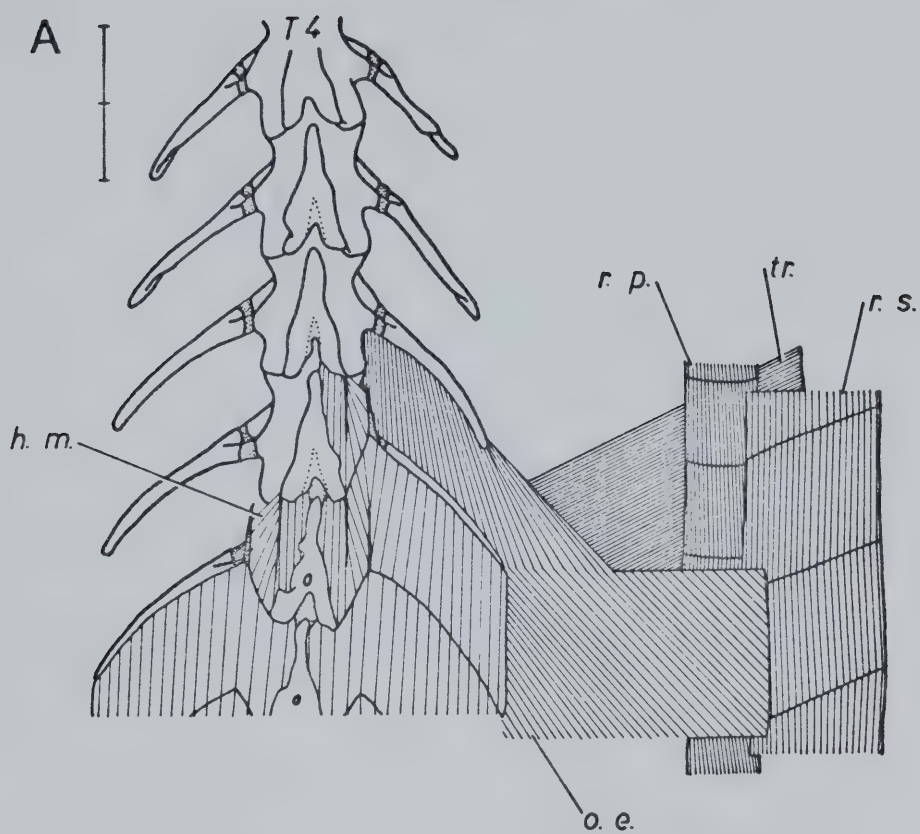


Figure 73. Dissection of metamorphosed adult *Notophthalmus viridescens* with lateral abdominal musculature spread laterally: (A) dorsal view; (B) ventral view; scale represents two millimeters; abbreviations given on pp. 4-7.

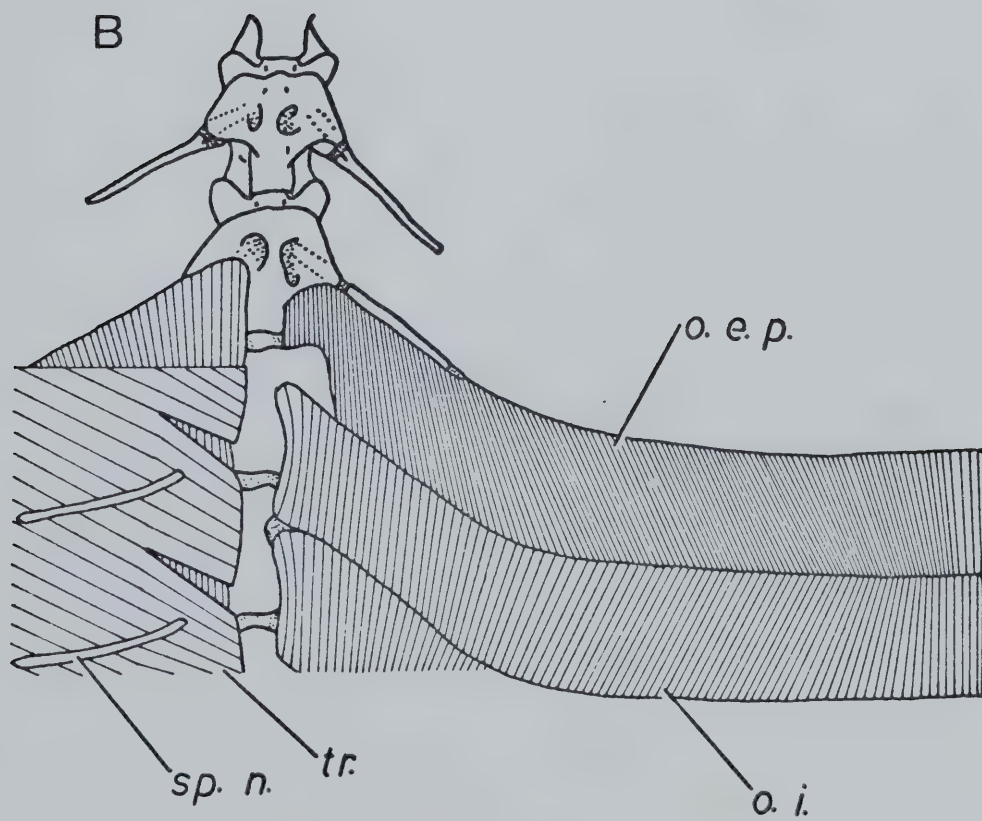
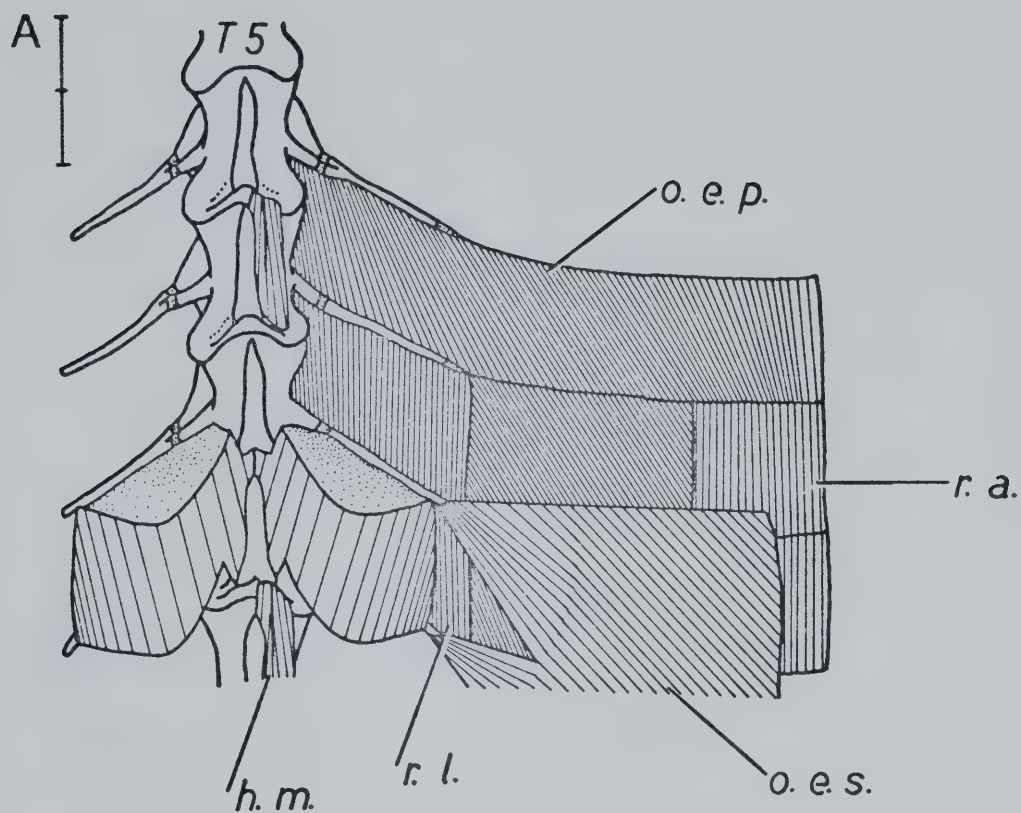


Figure 74. Dissection of neotenic adult *Notophthalmus viridescens* with lateral abdominal musculature spread laterally: (A) dorsal view; (B) ventral view, arrows marking ventral edge of *transversus*; scale represents two millimeters; abbreviations given on pp. 4-7.

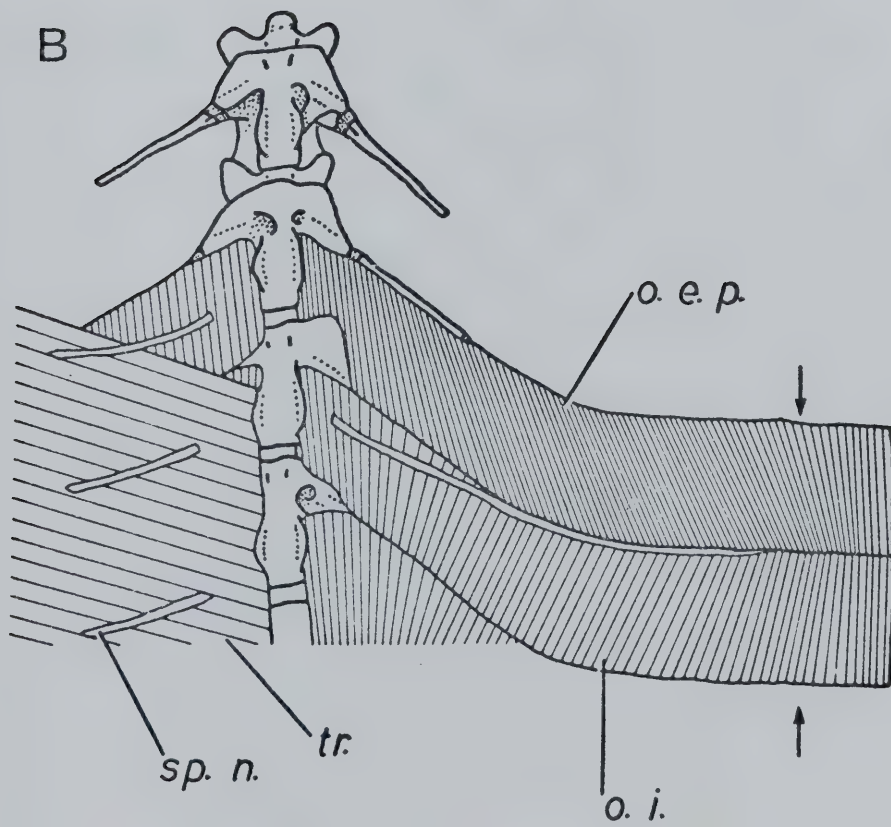
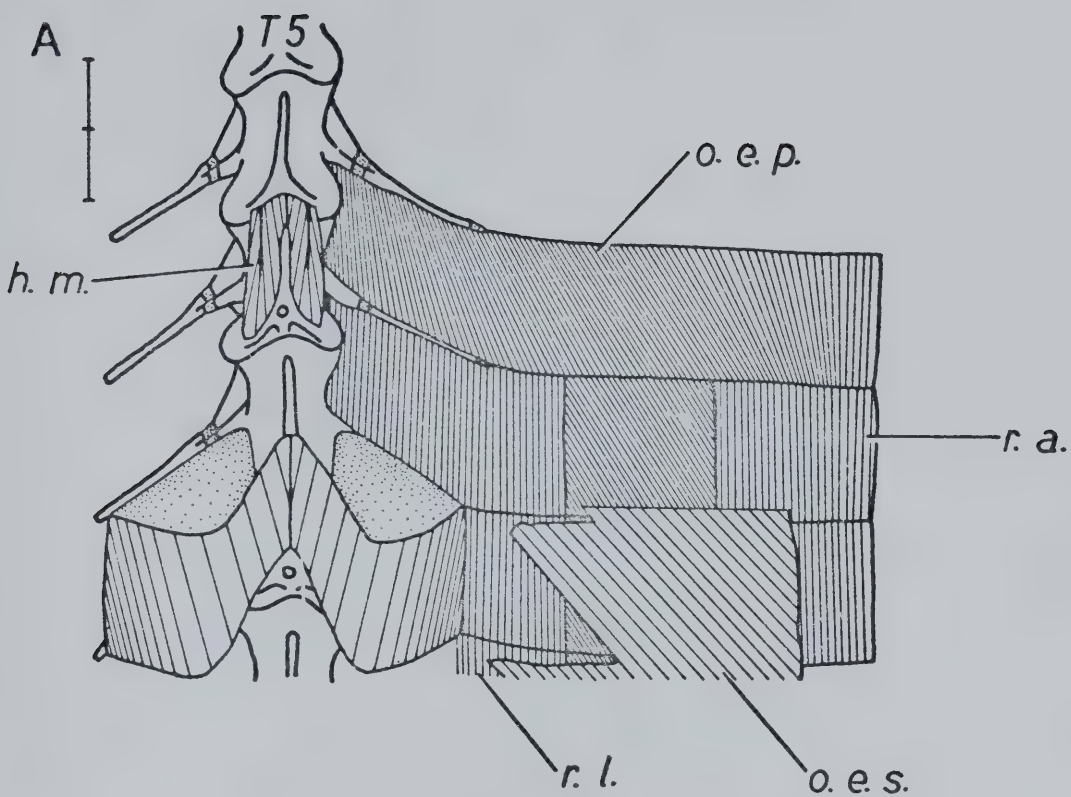
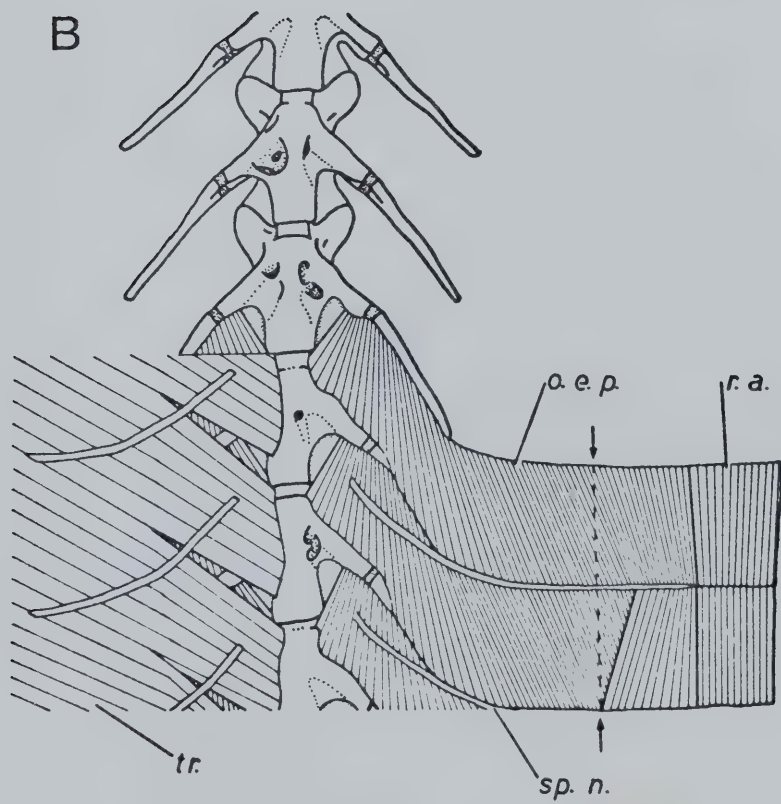
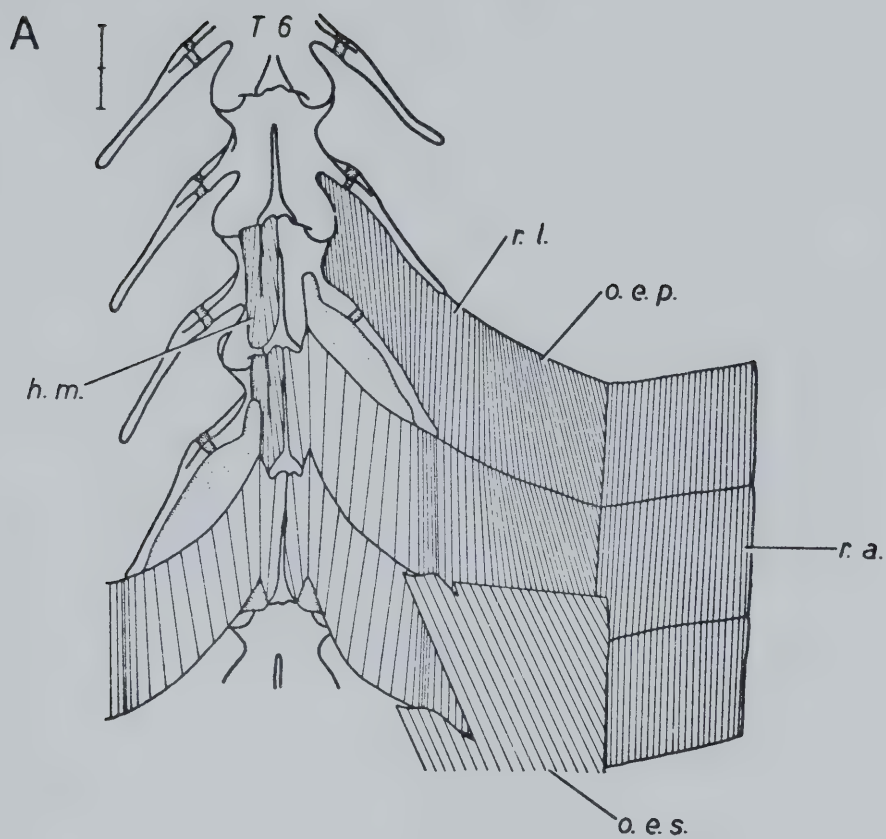


Figure 75. Dissection of *Taricha* species with lateral abdominal musculature spread laterally: (A) dorsal view; (B) ventral view, arrows and dotted line marking edge of *rectus abdominus*, which is not reflected in the direction of the muscle fibers, but is evident in anatomical specimens; scale represents two millimeters; abbreviations given on pp. 4-7.



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Figure 76. Dissection of *Cynops pyrrhogaster* with lateral abdominal musculature spread laterally: (A) dorsal view; (B) ventral view; scale represents two millimeters; abbreviations given on pp. 4-7.

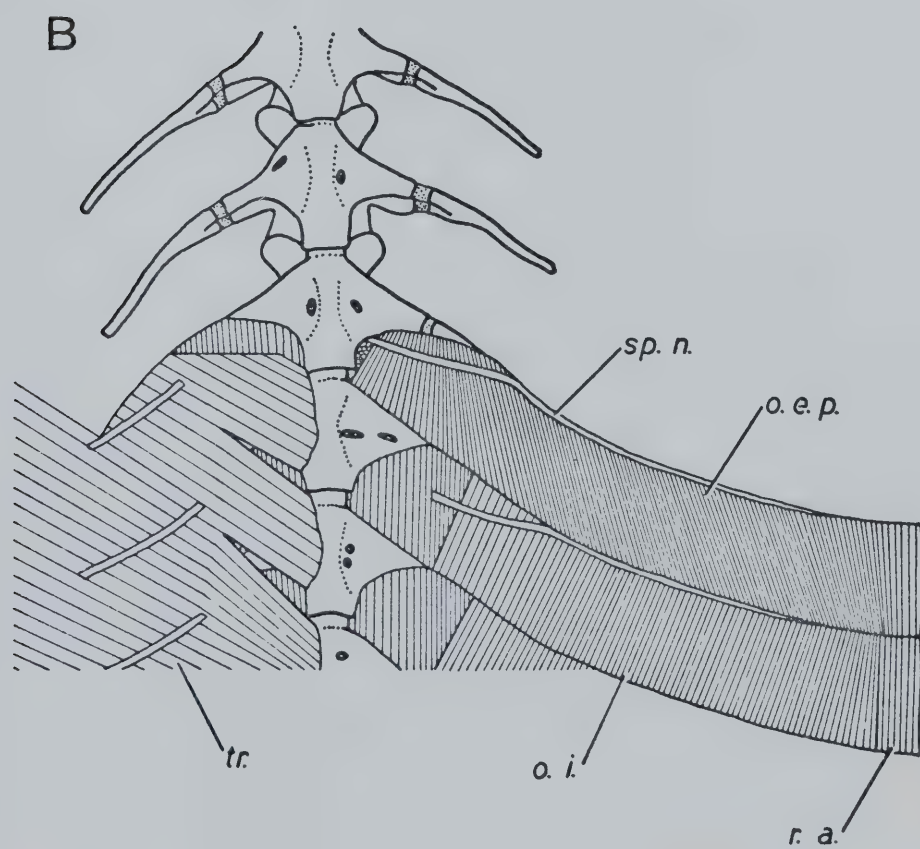
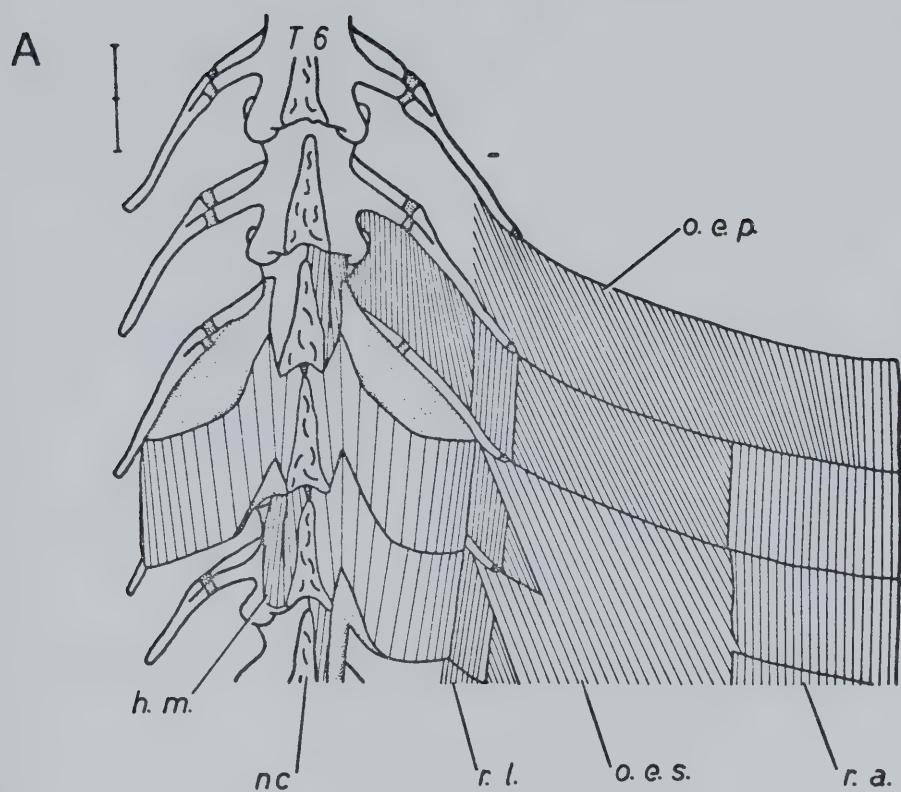


Figure 77. Dissection of *Paramesotriton hongkongense* with lateral abdominal musculature spread laterally: (A) dorsal view; (B) ventral view; scale represents two millimeters; abbreviations given on pp. 4-7.

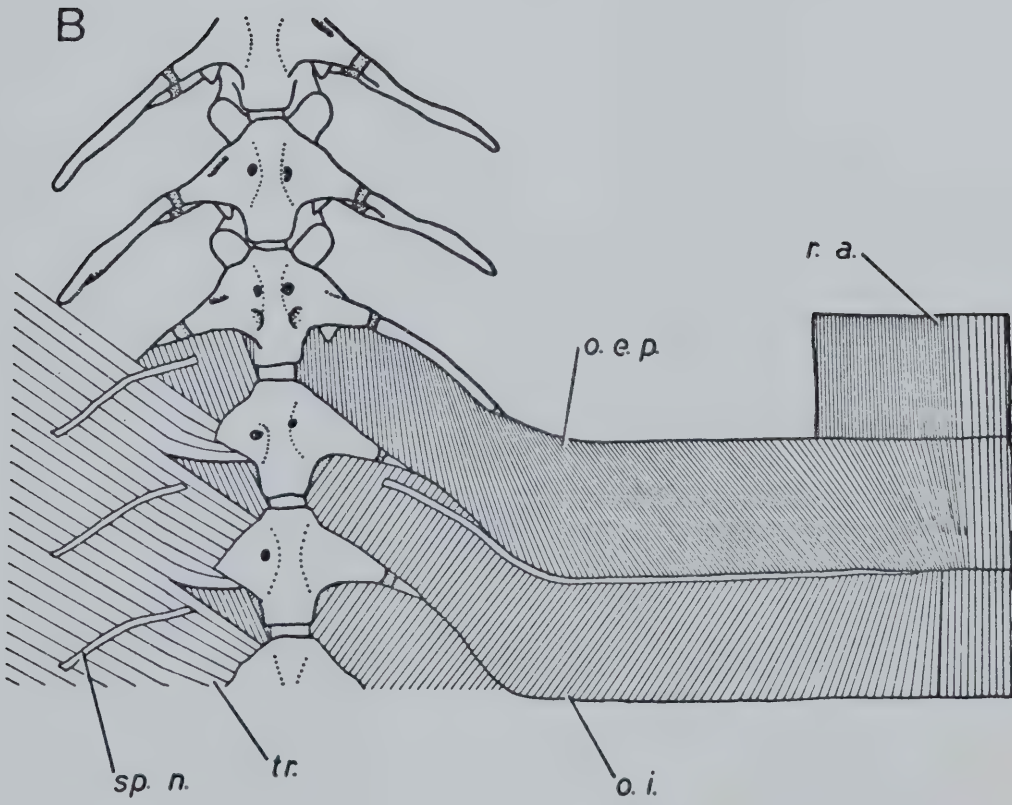
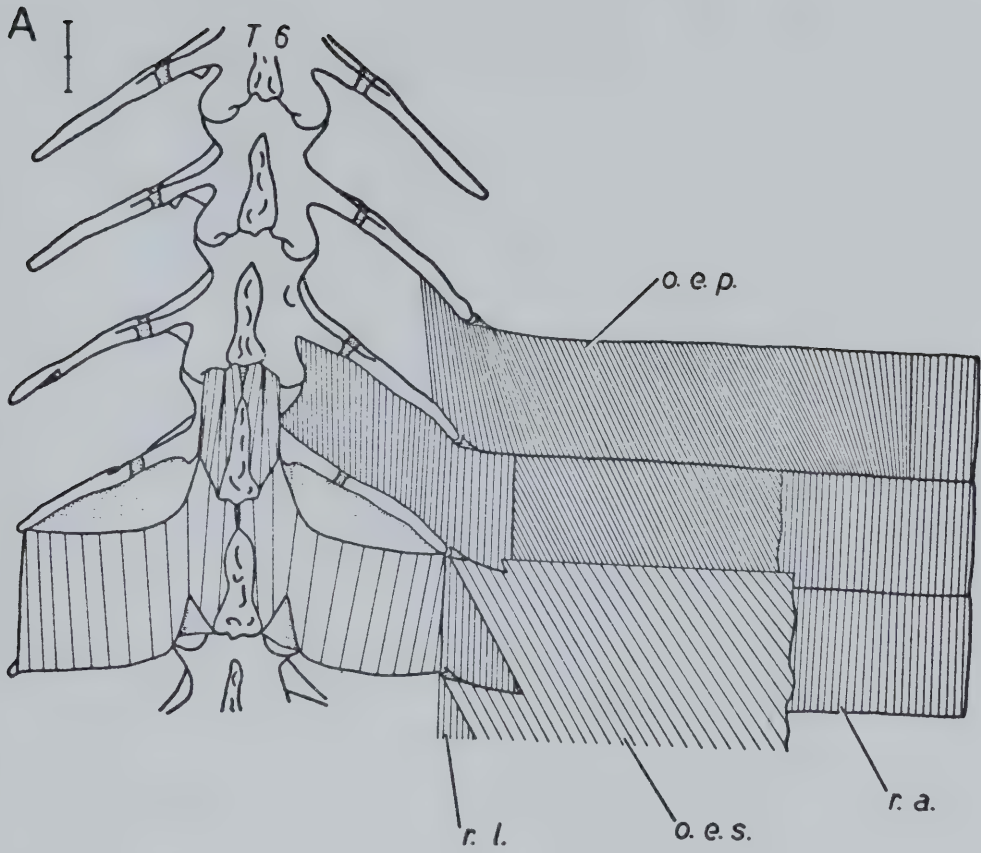


Figure 78. Dissection of *Triturus cristatus* with lateral abdominal musculature spread laterally: (A) dorsal view; (B) ventral view; scale represents two millimeters; abbreviations given on pp. 4-7.

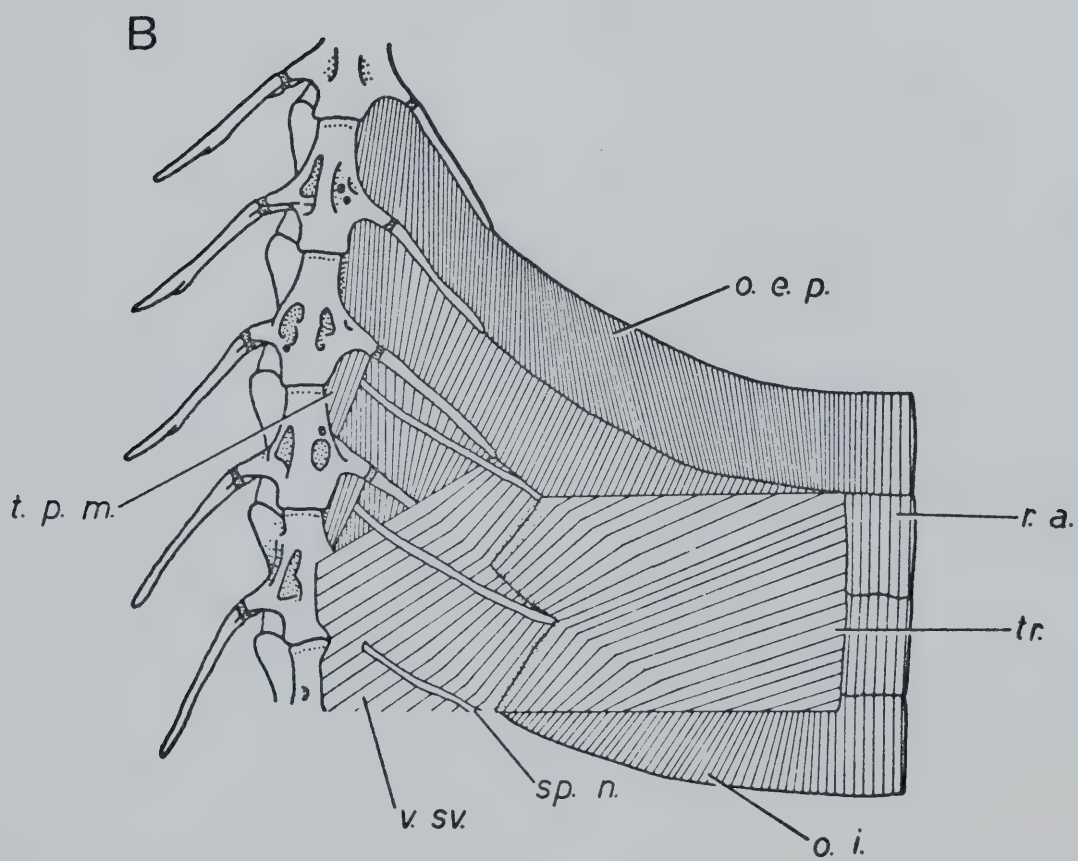
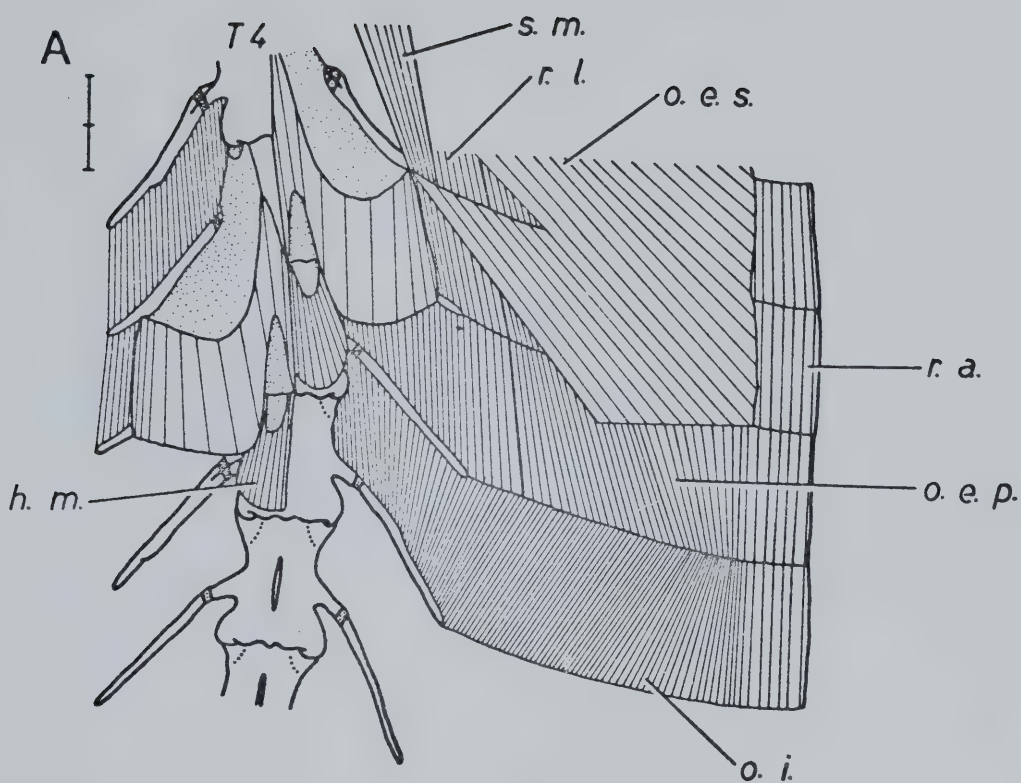


Figure 79. Dissection of a laterally flexed specimen of *Triturus marmoratus* with lateral abdominal musculature spread laterally: (A) dorsal view; (B) ventral view; scale represents two millimeters; abbreviations given on pp. 4-7.

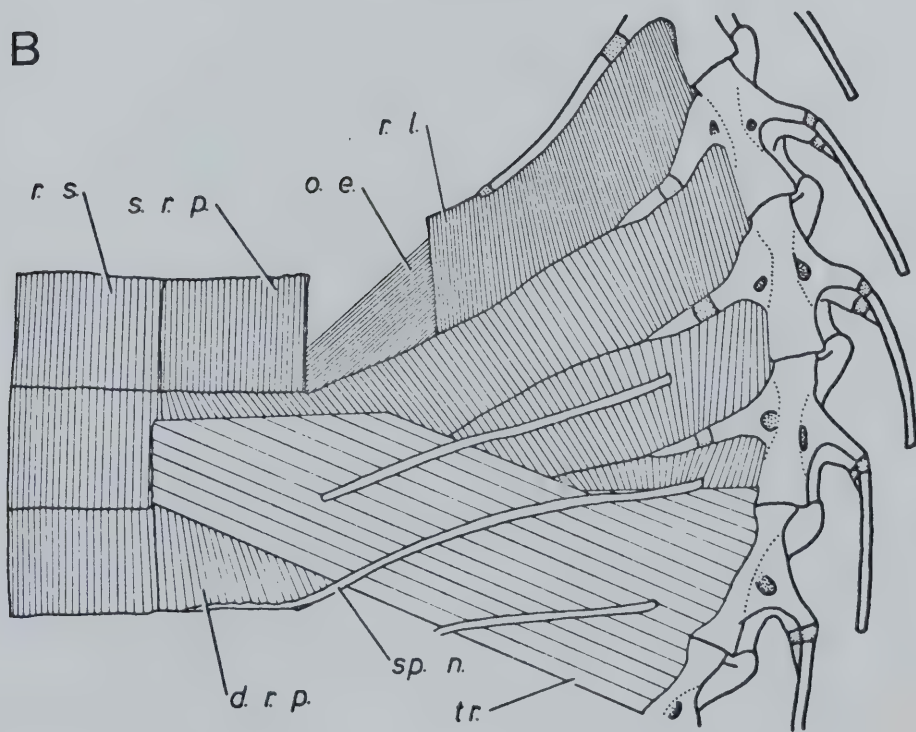
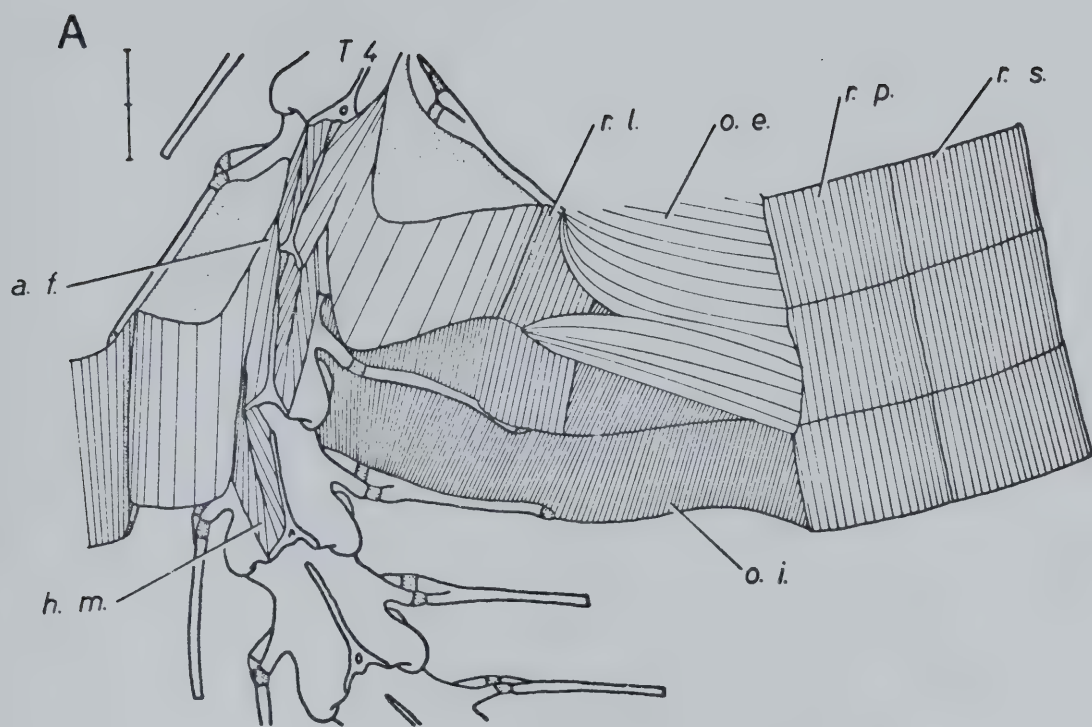


Figure 80. Dissection of *Triturus alpestris* with lateral abdominal musculature spread laterally: (A) dorsal view; (B) ventral view; scale represents two millimeters; abbreviations given on pp. 4-7.

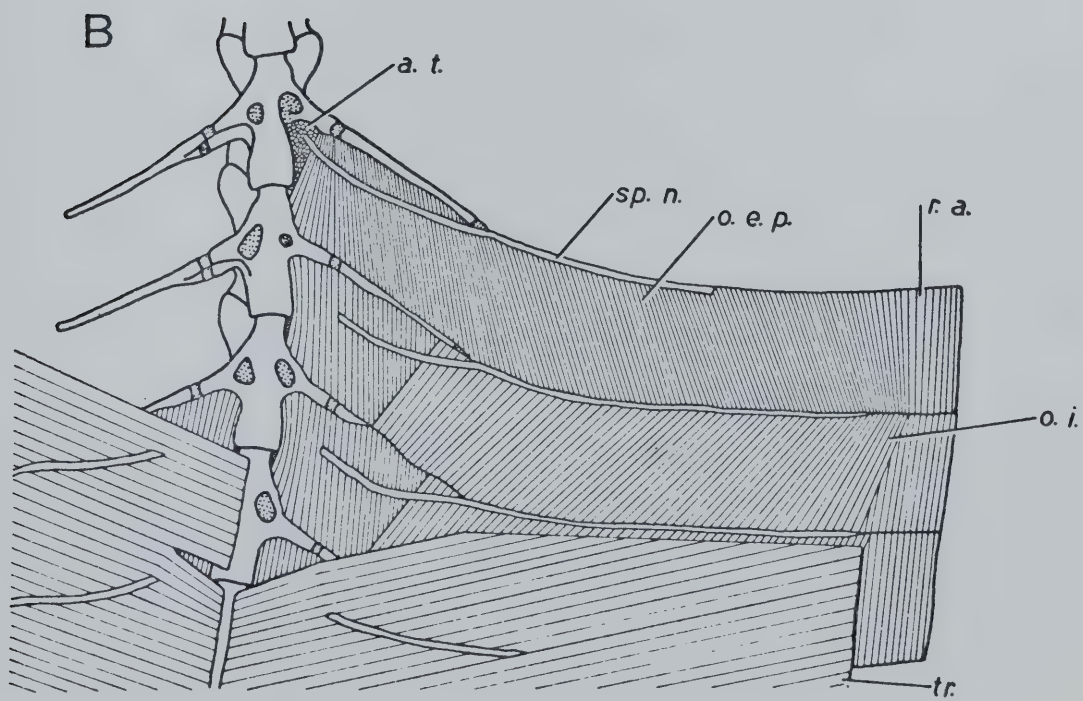
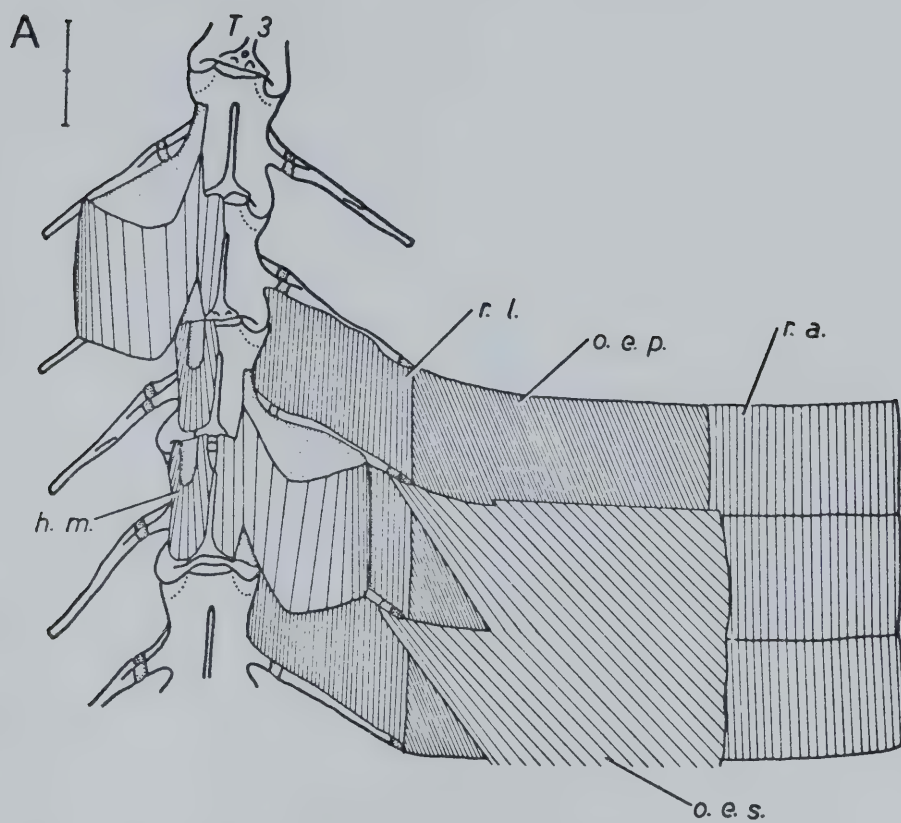


Figure 81. Dissection of *Triturus vittatus* with lateral abdominal musculature spread laterally: (A) dorsal view; (B) ventral view, arrow and dotted line showing questionable division into *rectus abdominus superficialis* and *rectus abdominus profundus*; scale represents two millimeters; abbreviations given on pp. 4-7.

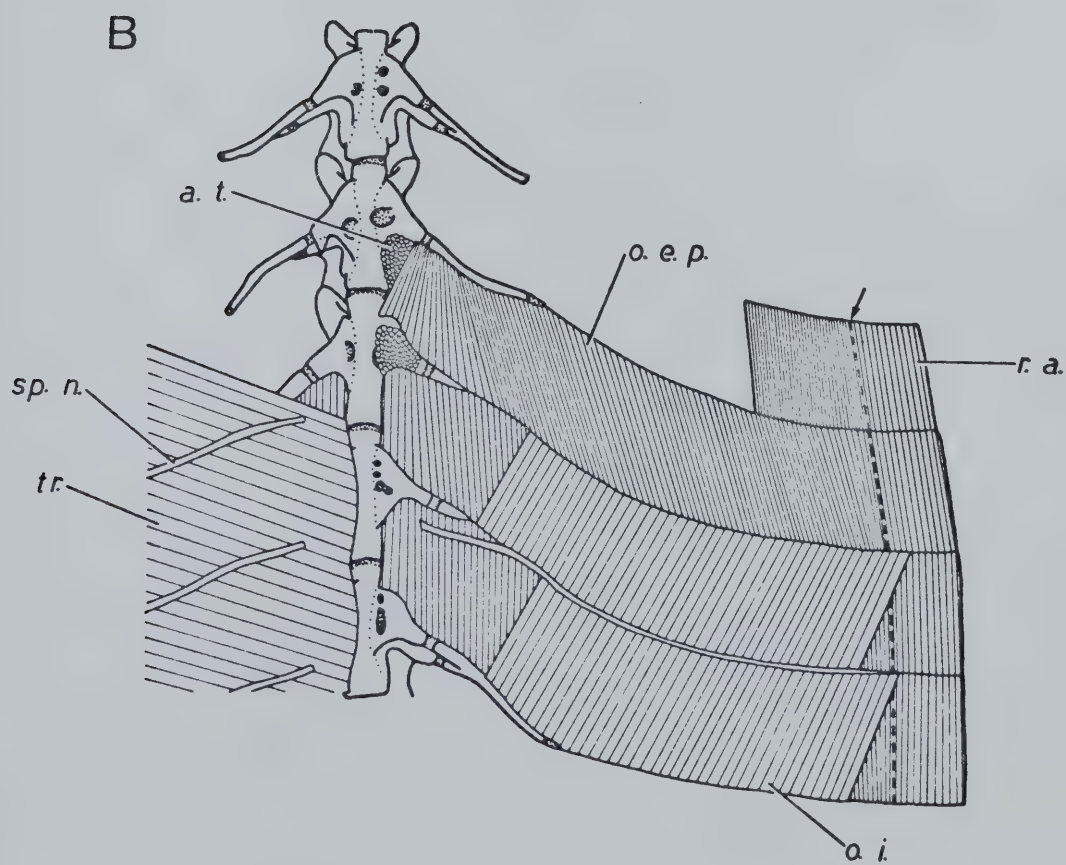
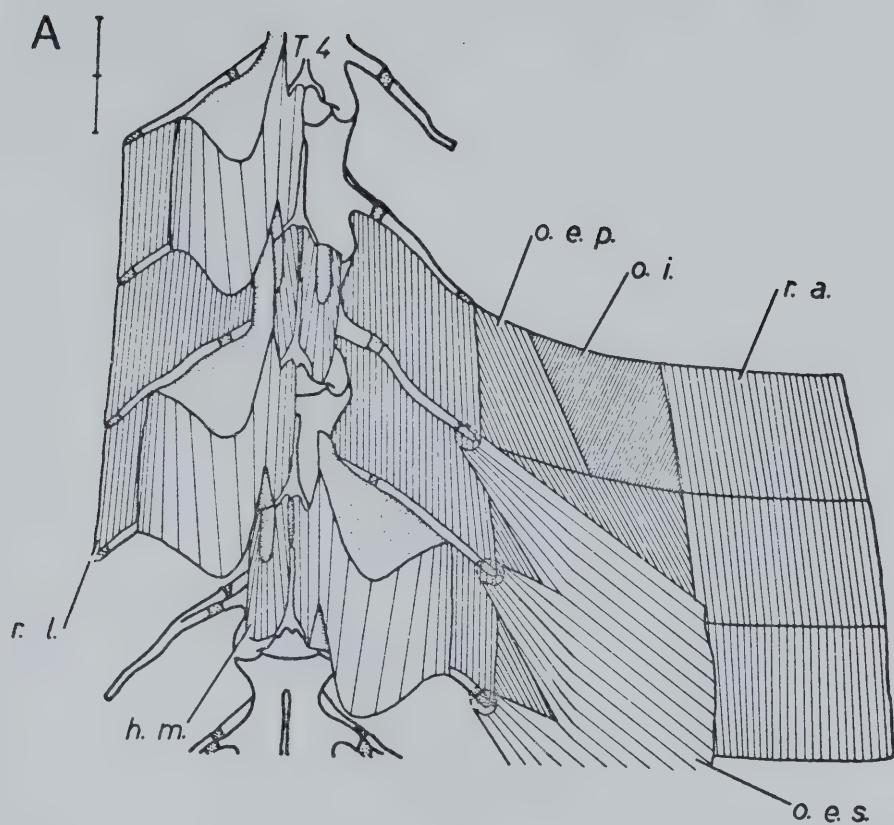


Figure 82. Dissection of *Triturus vulgaris* with lateral abdominal musculature spread laterally: (A) dorsal view; (B) ventral view; scale represents two millimeters; abbreviations given on pp. 4-7.

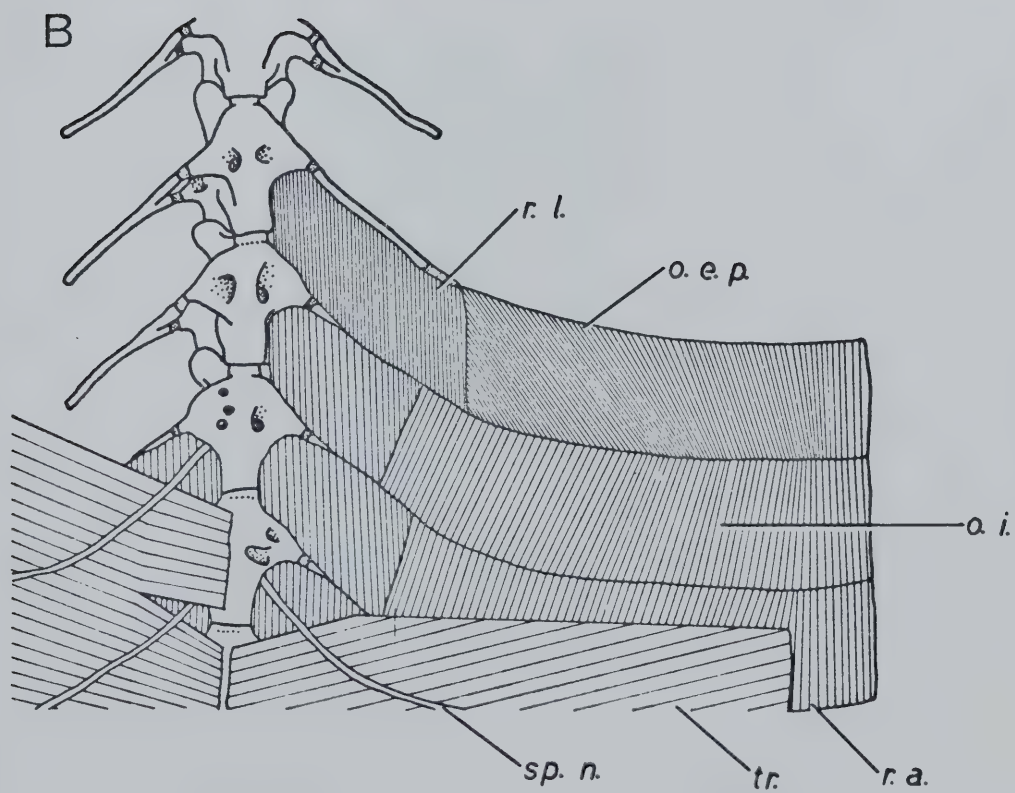
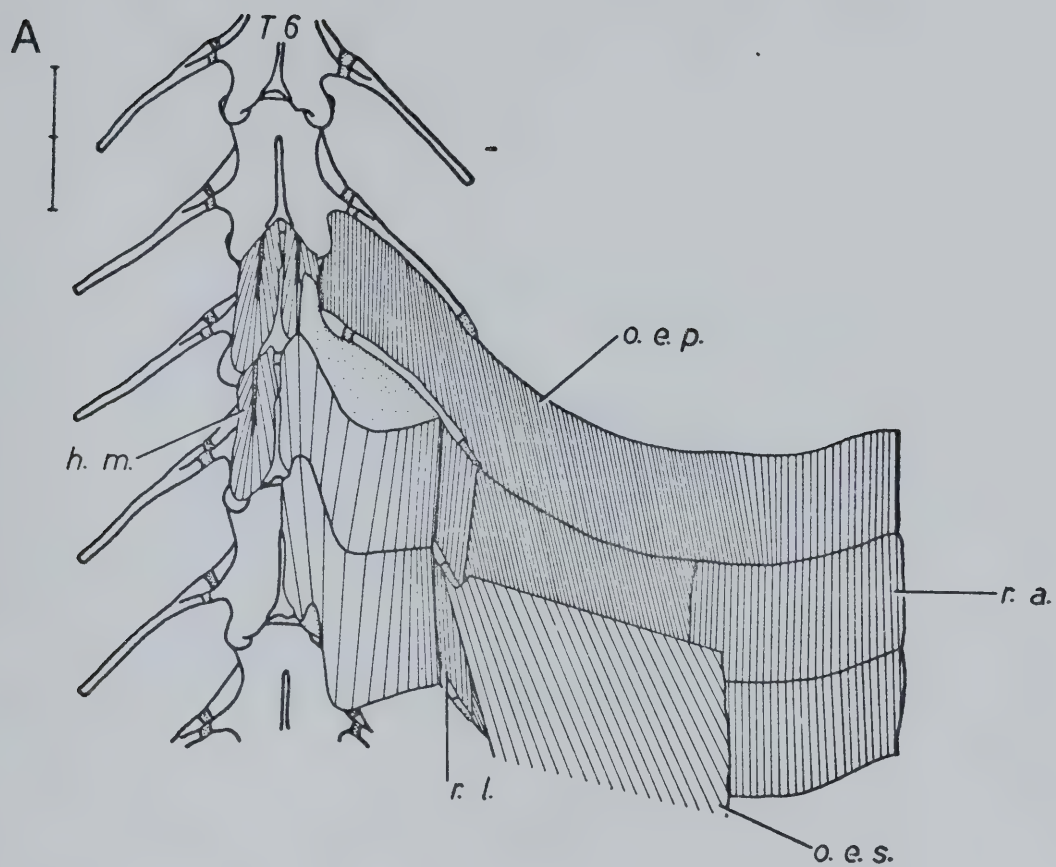
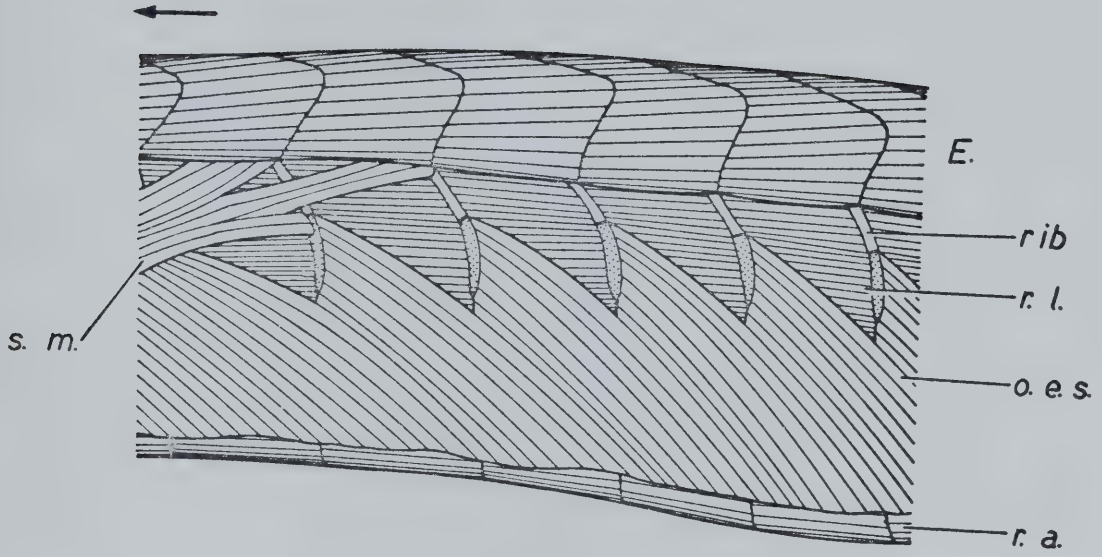


Figure 83. Camera lucida sketches of the anterior portion of the trunk of *Triturus vulgaris* just posterior of the pectoral girdle: (A) lateral view, arrow points anteriorly; (B) dorsal view, arrow points anteriorly; abbreviations given on pp. 4-7.

A



B

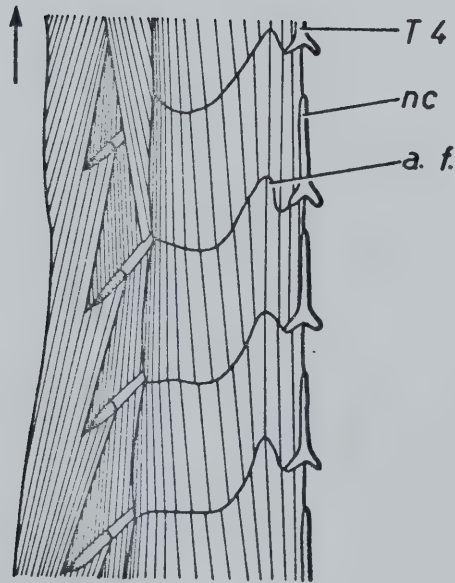


Figure 84. Dissection of *Triturus helveticus* with lateral abdominal musculature spread laterally: (A) dorsal view; (B) ventral view; scale represents two millimeters; abbreviations given on pp. 4-7.

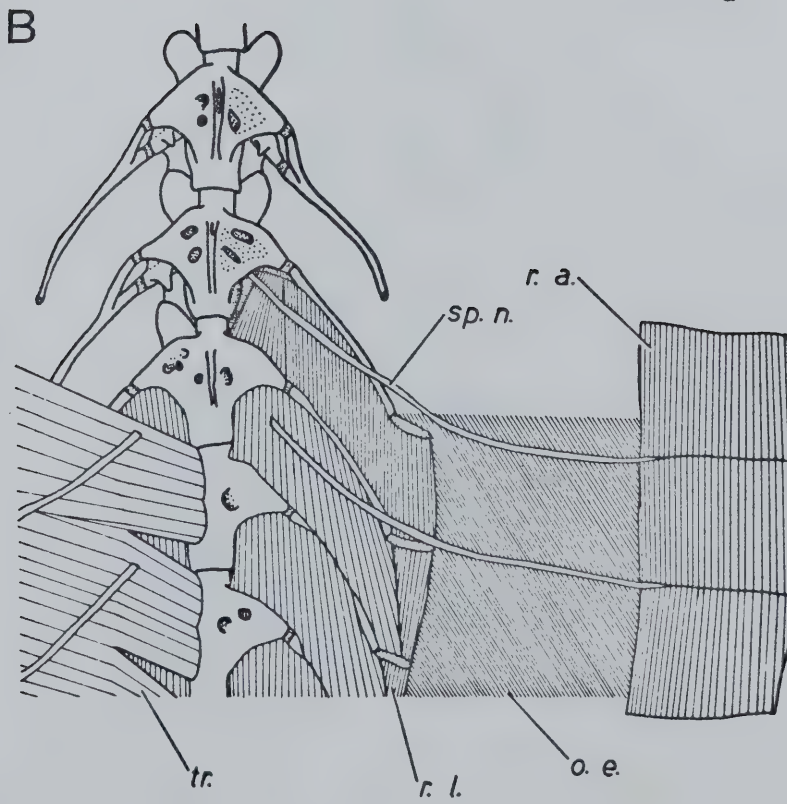
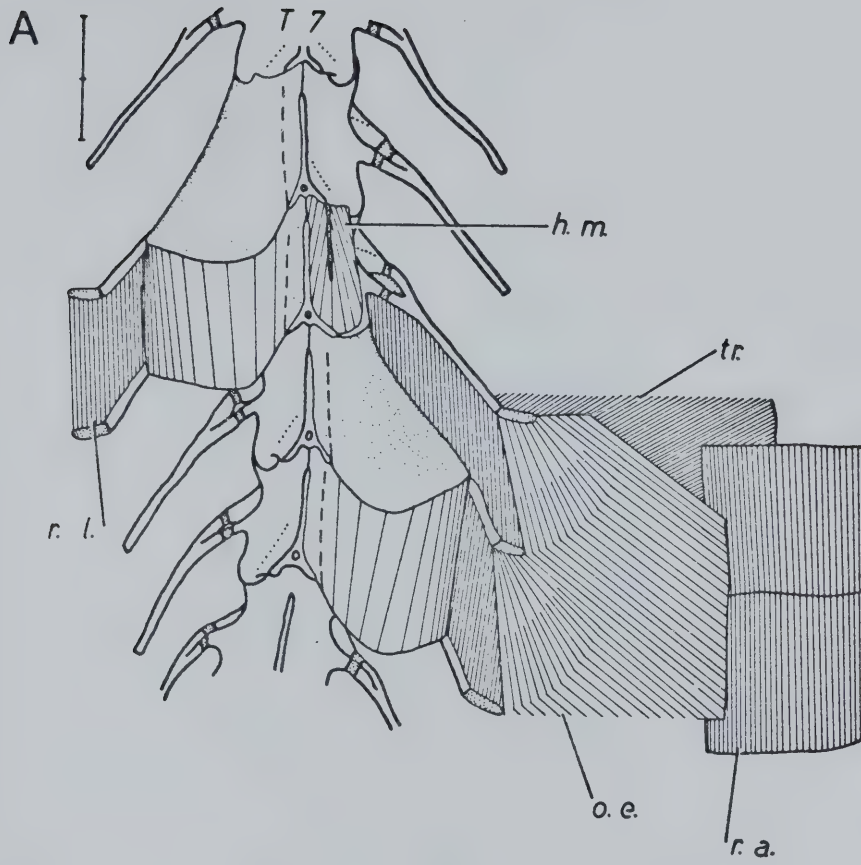


Figure 85. Dissection of *Euproctus asper* with lateral abdominal musculature largely omitted: (A) dorsal view; (B) ventral view; scale represents two millimeters; abbreviations given on pp. 4-7.

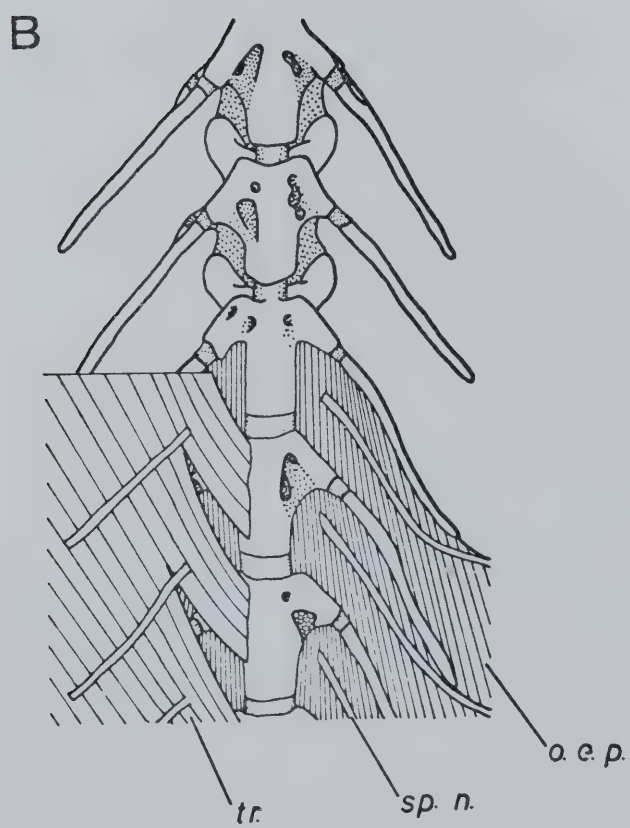
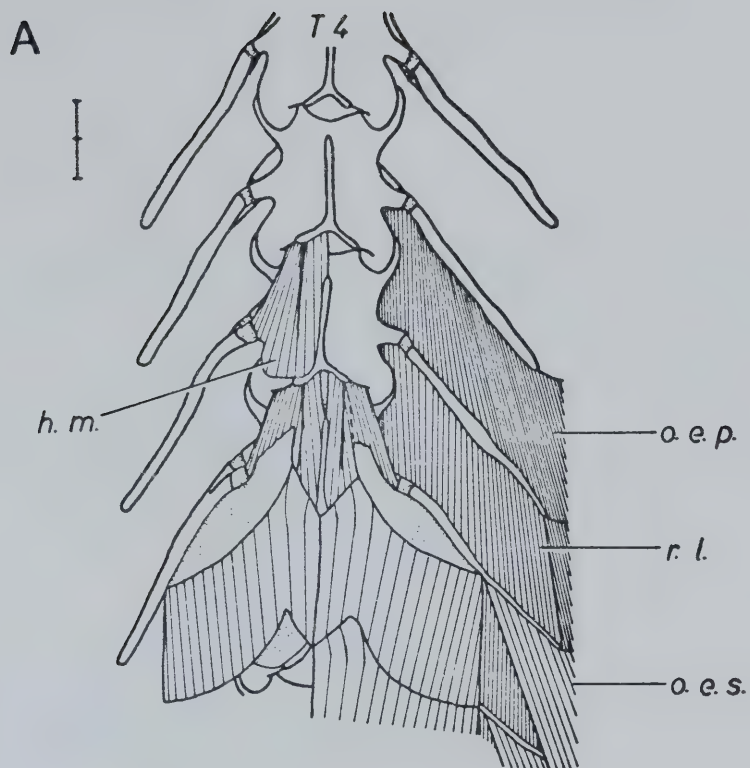
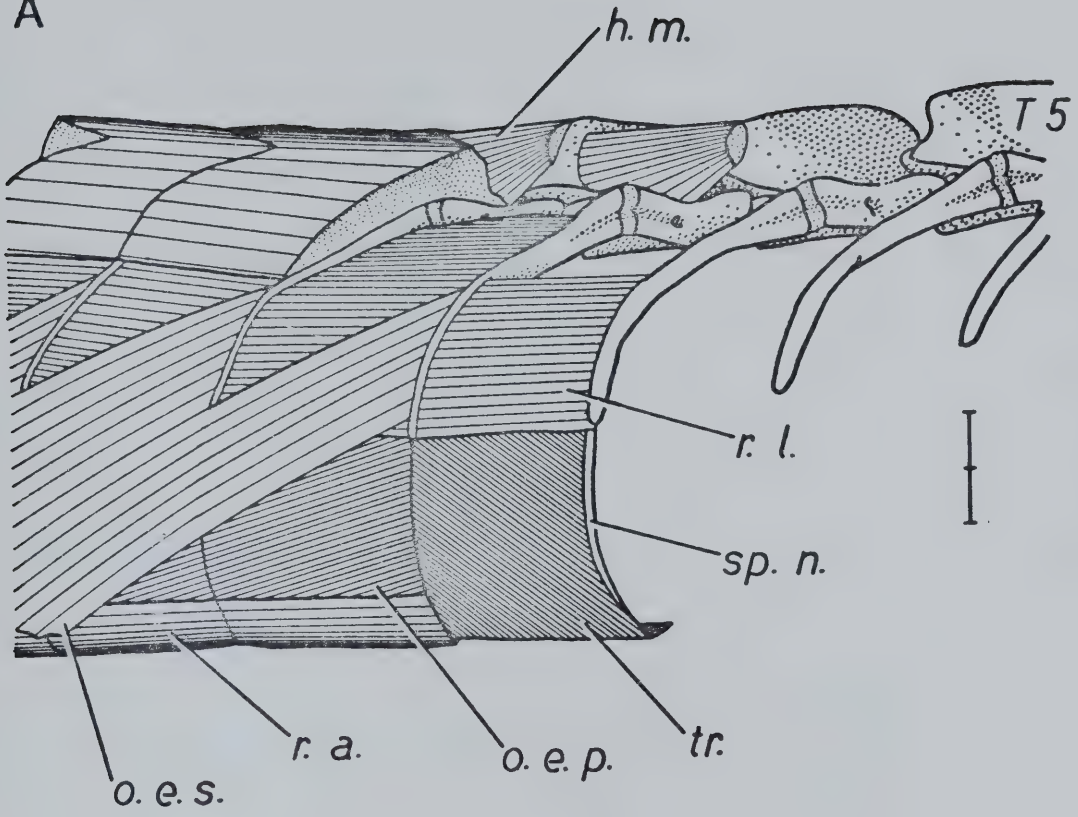


Figure 86. (A) lateral view of trunk of *Euproctus asper*, showing elongate ribs, scale represents two millimeters;
(B) vertebrae of *Taricha* species for comparison;
abbreviations given on pp. 4-7.

A



B

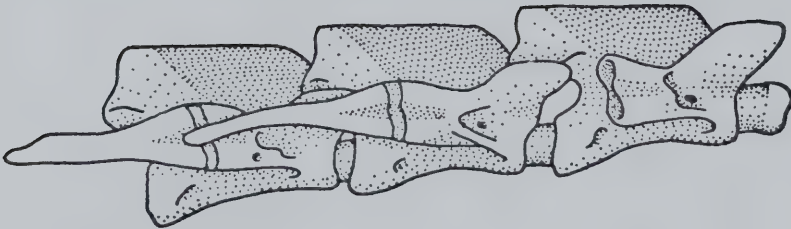


Figure 87. Dissection of *Siren lacertina*: (A) dorsal view of deep muscle units of the *dorsalis trunci*; (B) ventral view, lateral abdominal musculature spread laterally; scale represents two millimeters; abbreviations given on pp. 4-7.

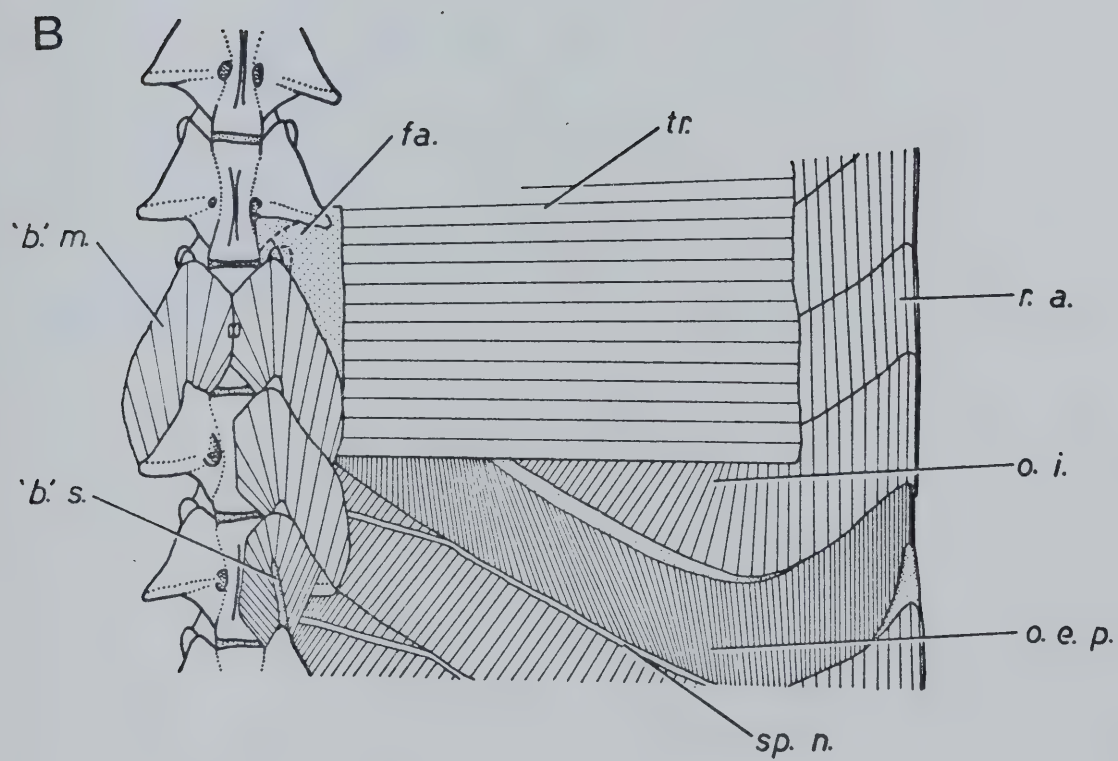
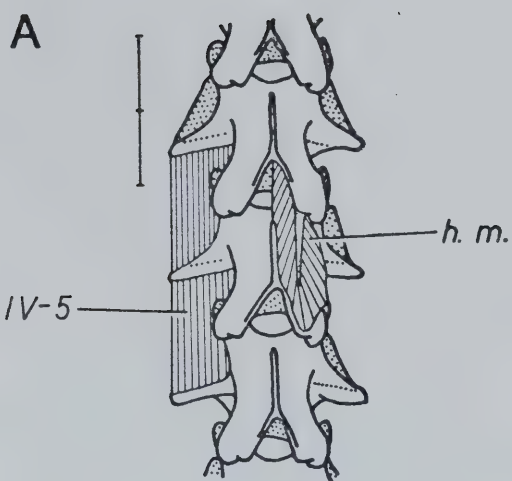


Figure 88. Camera lucida sketch of partially dissected trunk of *Siren intermedia* in lateral view, anterior to left; scale represents two millimeters; abbreviations given on pp. 4-7.

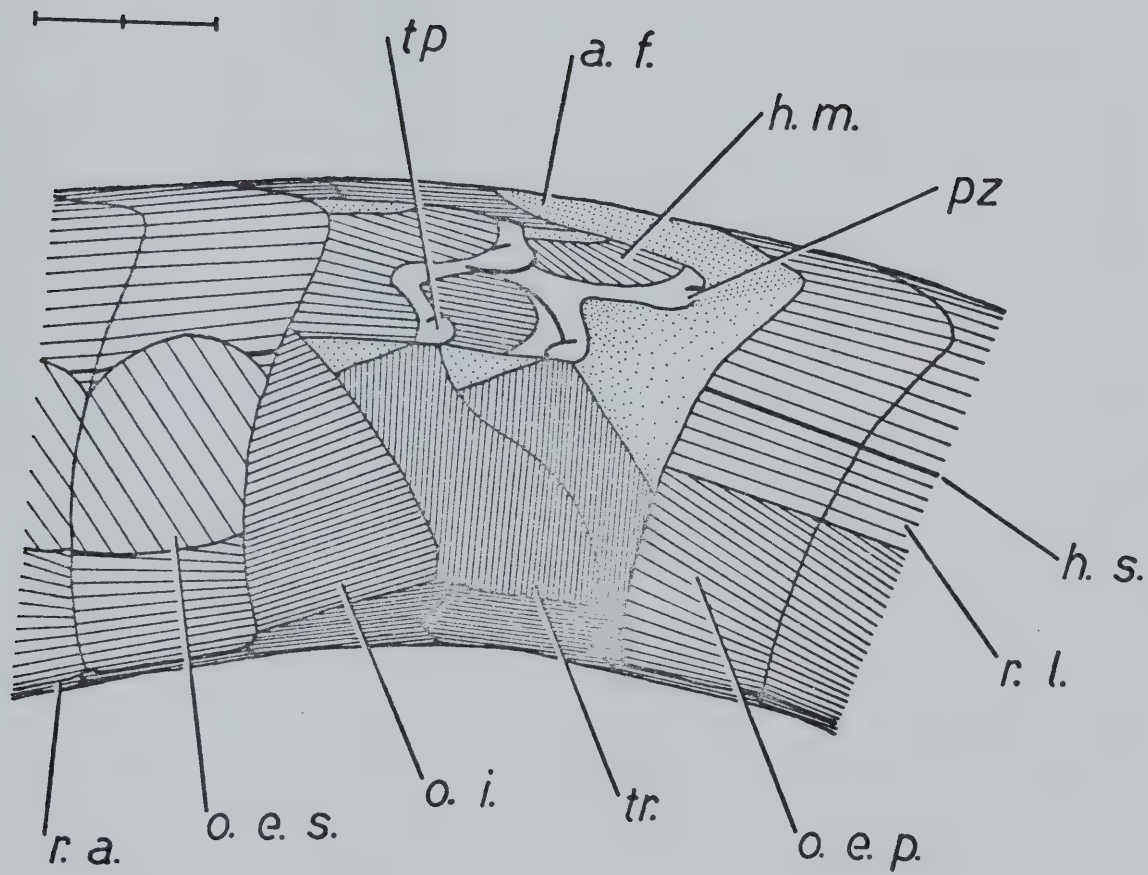


Figure 89. Cross-section through the trunk musculature of large adult *Siren lacertina* drawn with camera lucida; scale represents two millimeters; abbreviations given on pp. 4-7.

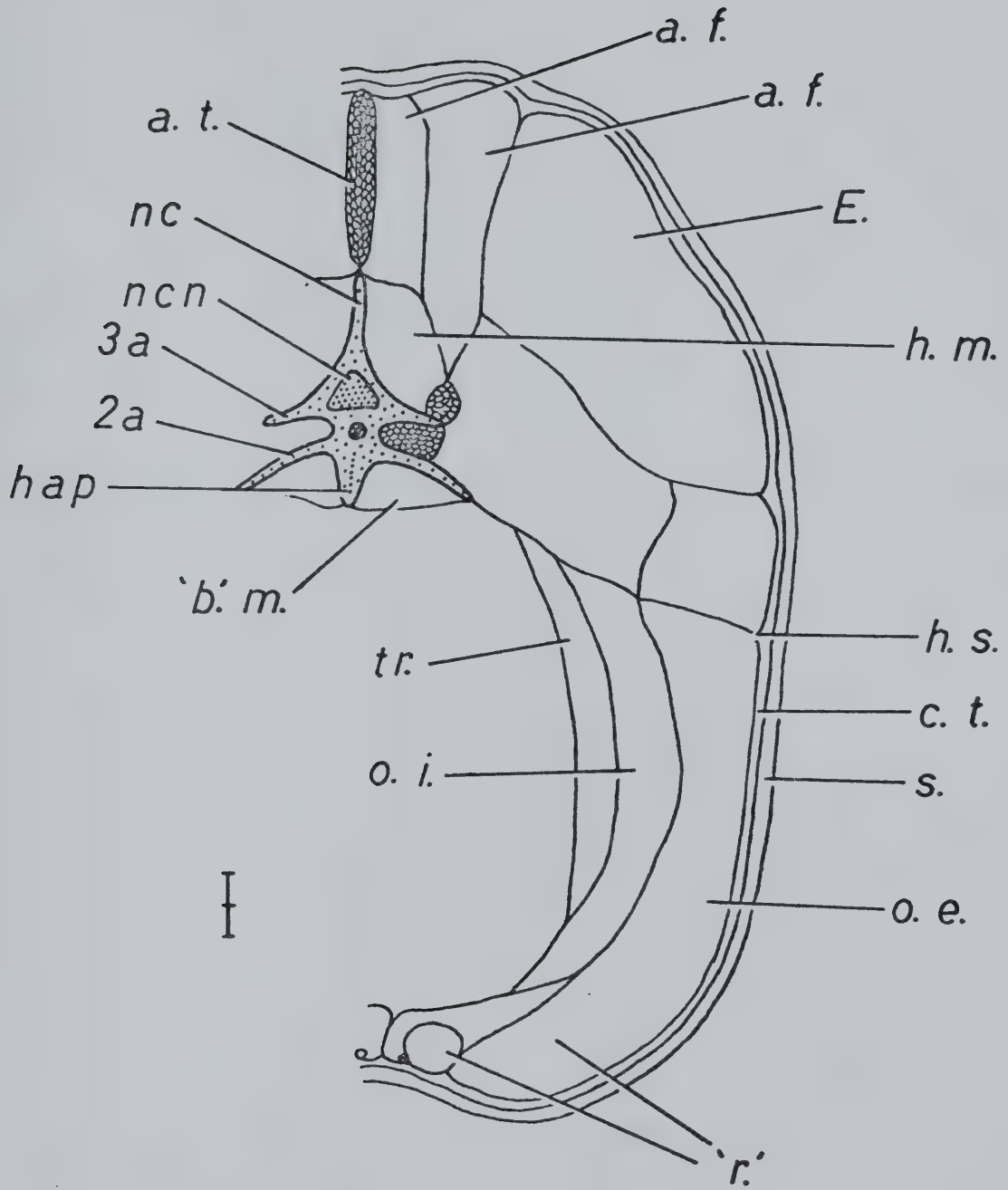


Figure 90. Genera of ambystomatids, plethodontids, and salamandrids forming a morphocline with respect to the *subvertebralis*; see text for discussion.

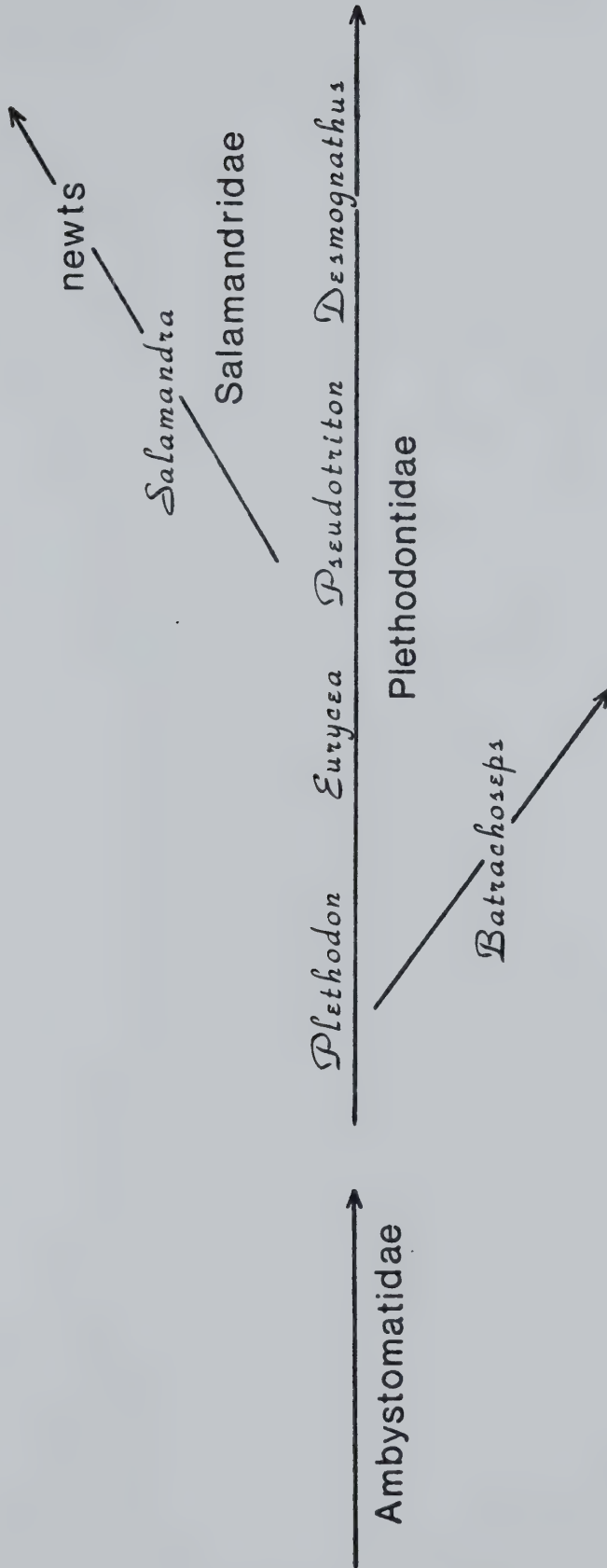


Figure 91. Cladistic and evolutionary relationships of a series of hypothetical taxa, after Schaeffer, Hecht, and Eldredge (1972); see text for discussion.

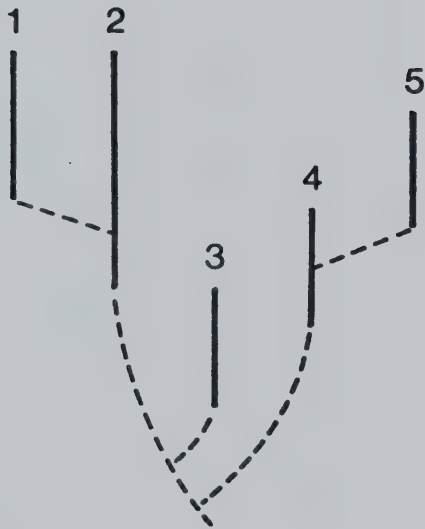
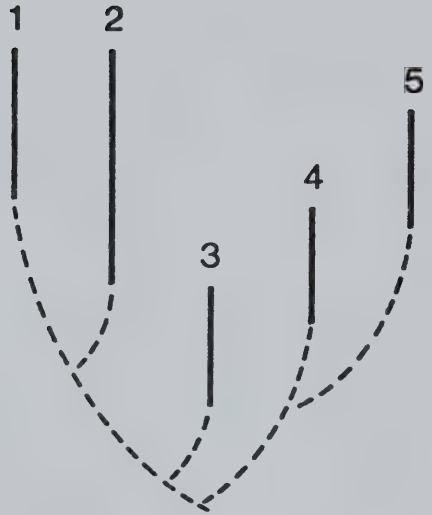
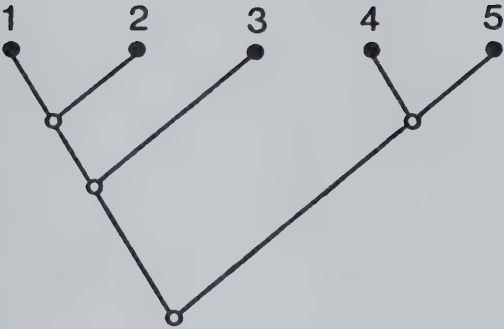


Figure 92. A group of related taxa with the long rectangles
indicating shared characters (primitive or derived);
see text for discussion.

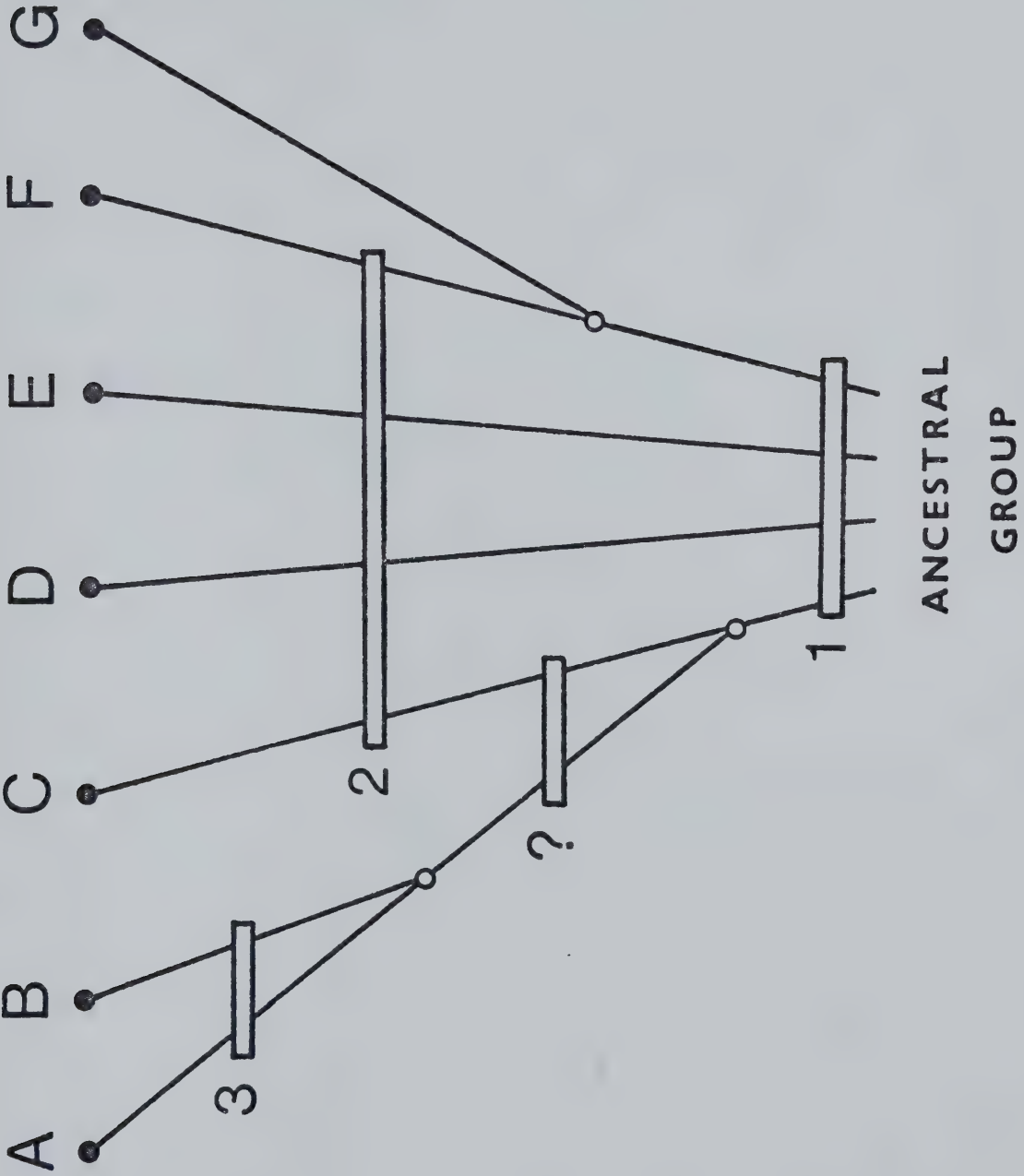
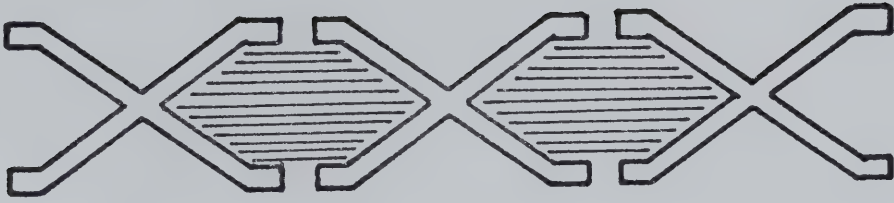


Figure 93. Diagrammatic longitudinal sections across intercentral joints in salamanders, horizontal lines representing notochordal tissue: (A) fully amphicoelous, most primitive; (B) modified amphicoelous with infilling of the cotyles, as in scapherpetontids and amphiumids; (C) opisthocoelous, forming a strengthened joint; (D) opisthocoelous, forming a true ball-and-socket joint.

A



B



C

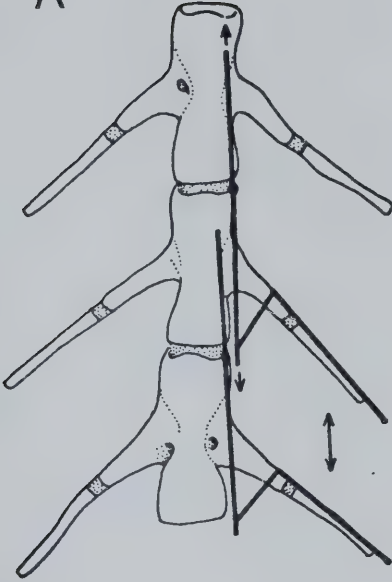


D

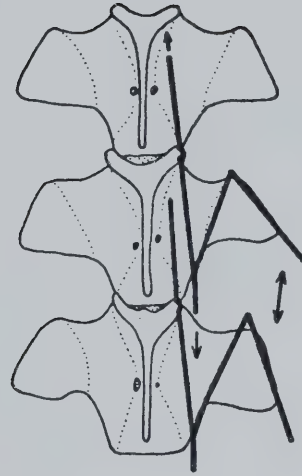


Figure 94. Ventral view of midtrunk vertebrae showing different septal patterns of the *subvertebralis*: (A) *Ambystoma jeffersonianum*, basic anterior basapophyseal pattern; (B) *Amphiuma tridactylum*, modified anterior basapophyseal pattern; (C) *Plethodon jordani*, transitional between anterior and posterior basapophyseal patterns; (D) *Plethodon glutinosus*, basic posterior basapophyseal pattern; arrows show directions of pull on and between septa.

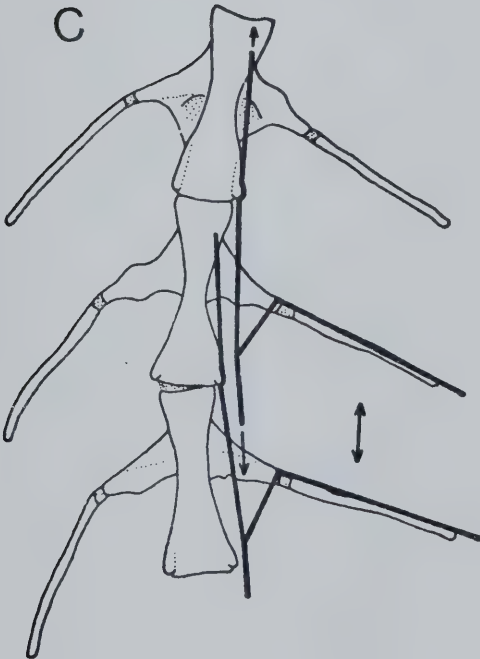
A



B



C



D

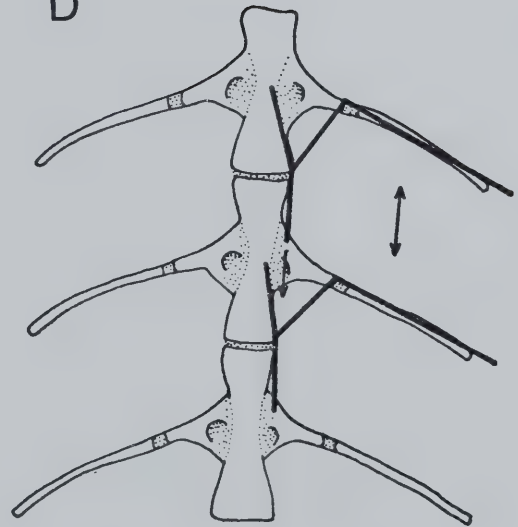


Figure 95. Ventral views of midtrunk vertebrae showing septal patterns of the *subvertebralis* in neocaudates:

(A) *Gyrinophilus*; (B) *Pseudotriton*; (C) *Desmognathus*, full development of posterior basapophyseal muscle;

(D) *Batrachoseps attenuatus*, suppression of subvertebral septa and flexures; arrows show directions of pull on and between septa.

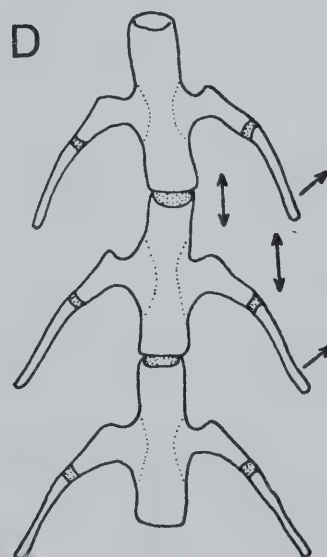
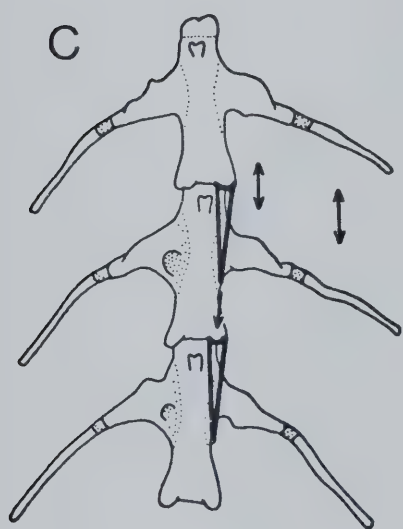
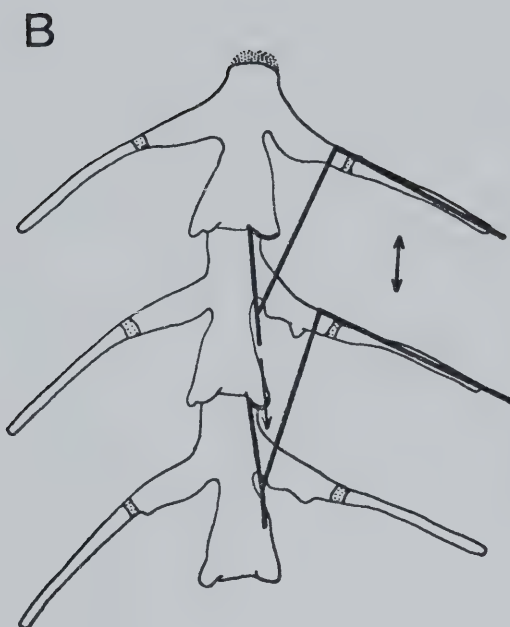
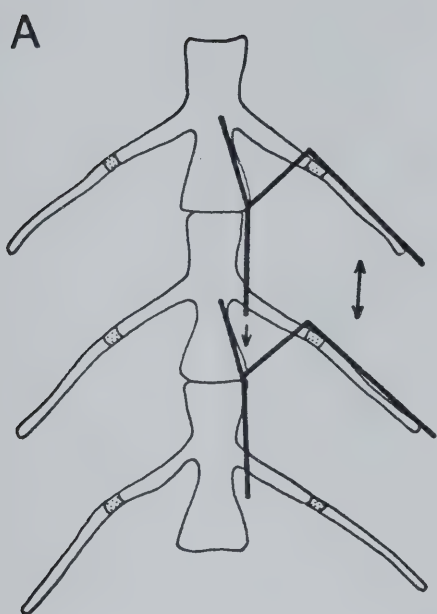


Figure 96.. Ventral view of midtrunk vertebrae showing septal patterns of the *subvertebralis* in derived Neocaudates:
(A) *Salamandra salamandra* (B) *Necturus maculosus*;
arrows show directions of pull on and between septa.

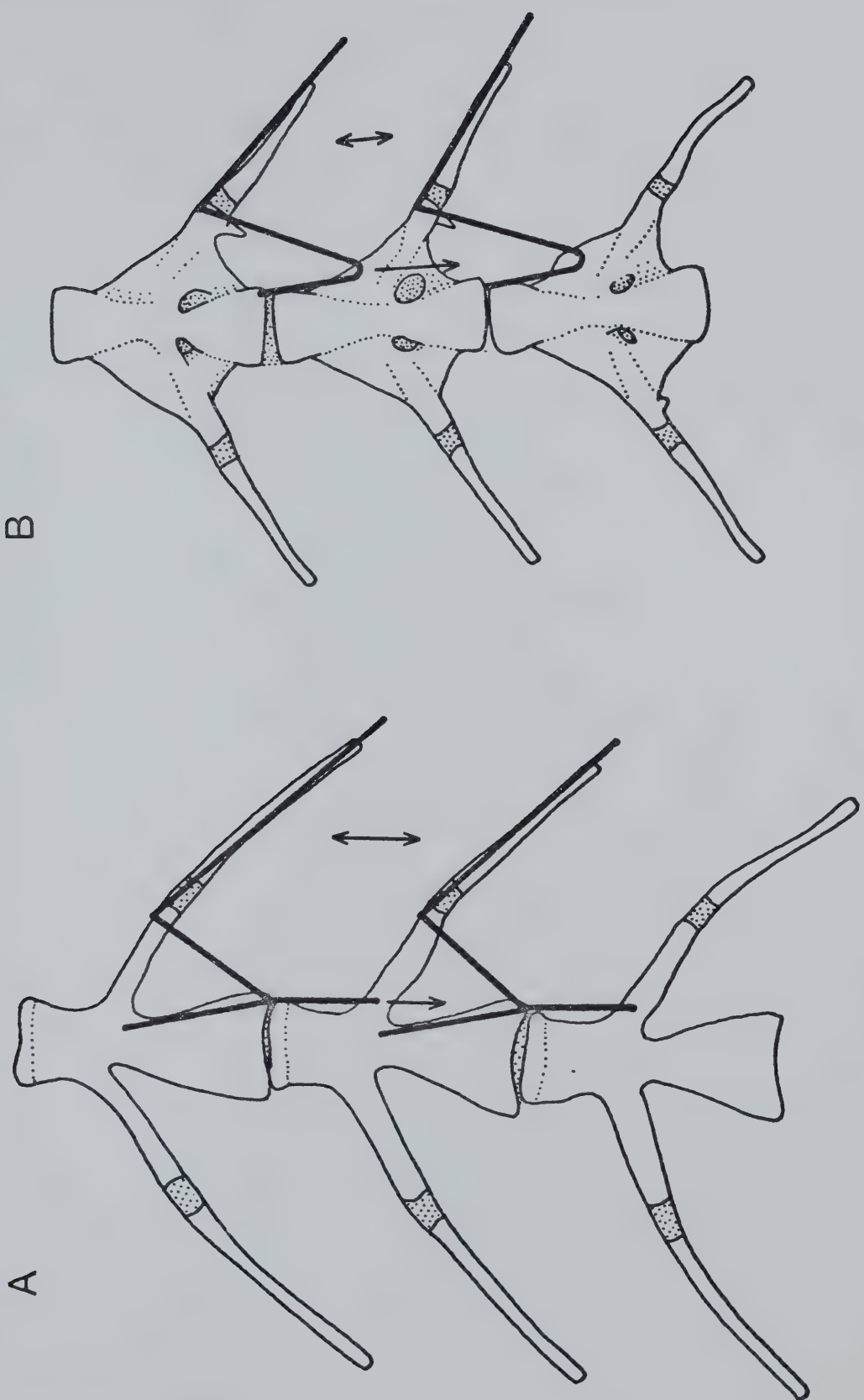


Figure 97. Ventral views of midtrunk vertebrae showing directions of muscle action in animals that have lost subvertebral flexures: (A) *Triturus helveticus*, showing pattern of the opisthocoelous newts; (B) *Siren*, showing secondary development of a "basapophyseal" muscle, probably from the situation seen in newts; (C) a lizard, showing convergence in a procoelous reptile with the opisthocoelous newts.

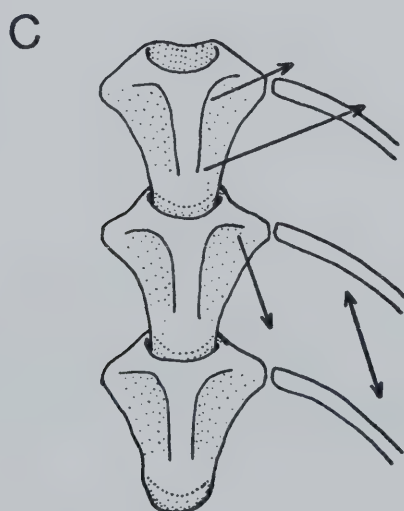
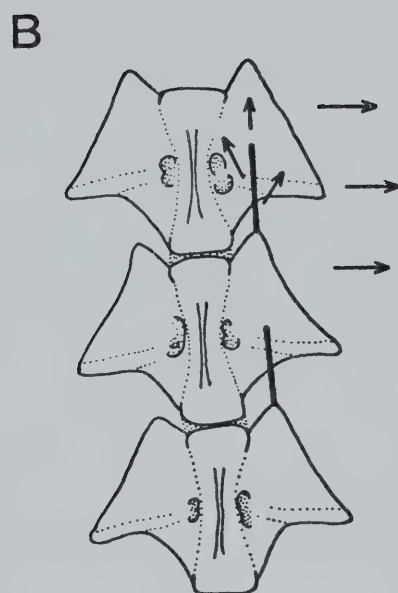
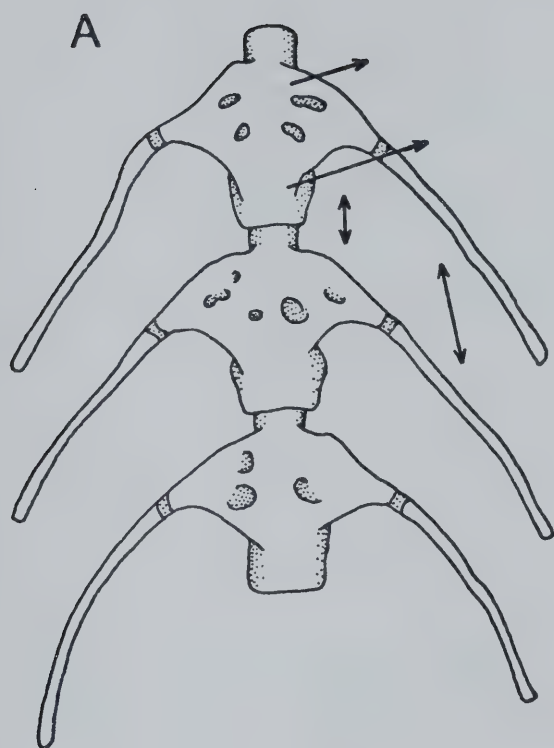


Figure 98. Left dentary (UA 14316) referred to *Proamphiuma cretacea*;
from the Bug Creek Anthills locality, Upper Cretaceous
Hell Creek Formation, Montana.

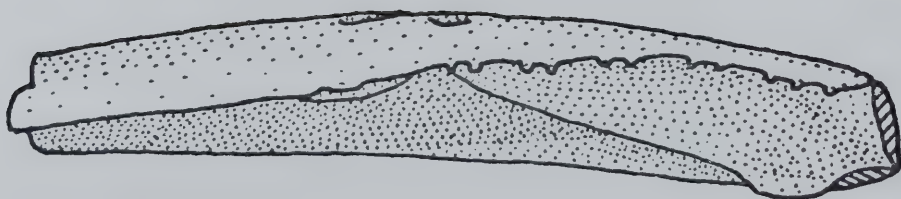
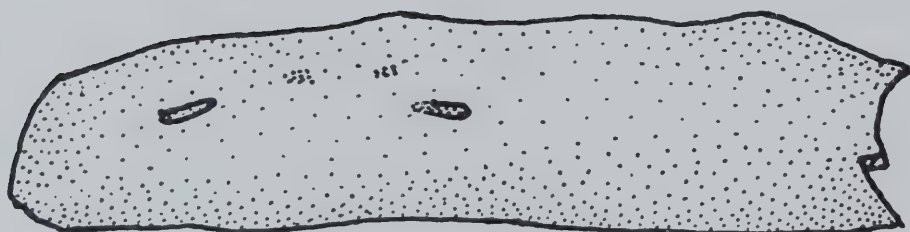
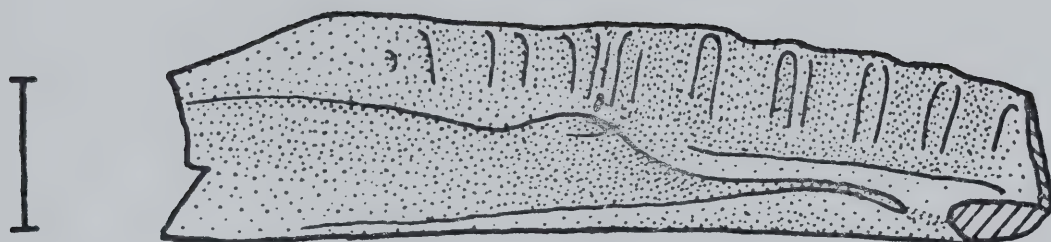


Figure 99. Proposed cladistic relationships within the family Ambystomatidae; species groups differ from those of Tihen (1958), being defined in the text and in Table 1; see text for discussion.

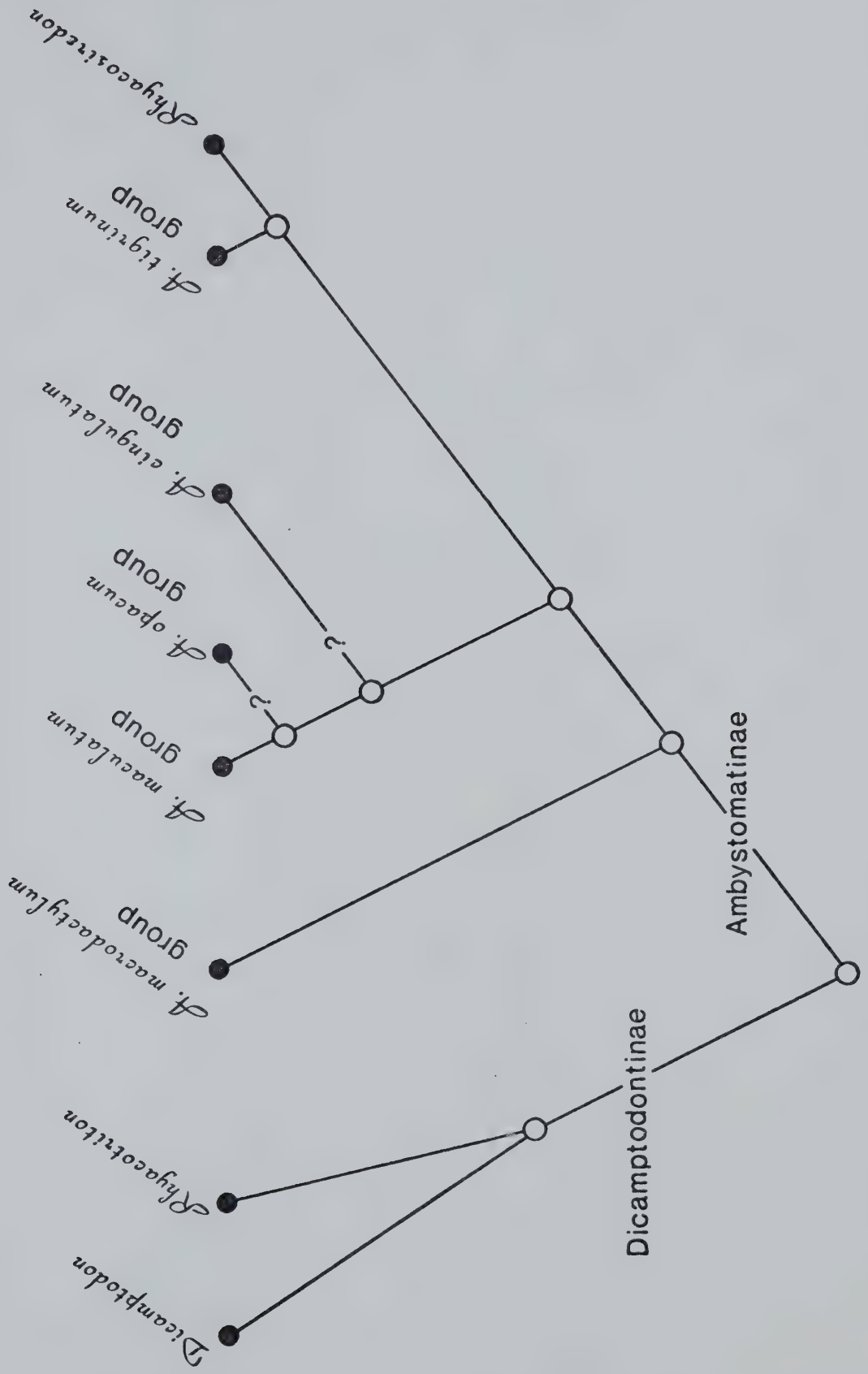


Figure 100. Proposed cladistic relationships within the family Plethodontidae; tribes and subfamilies differ from those of Wake (1966), being defined in the text and in Table 2; see text for discussion.

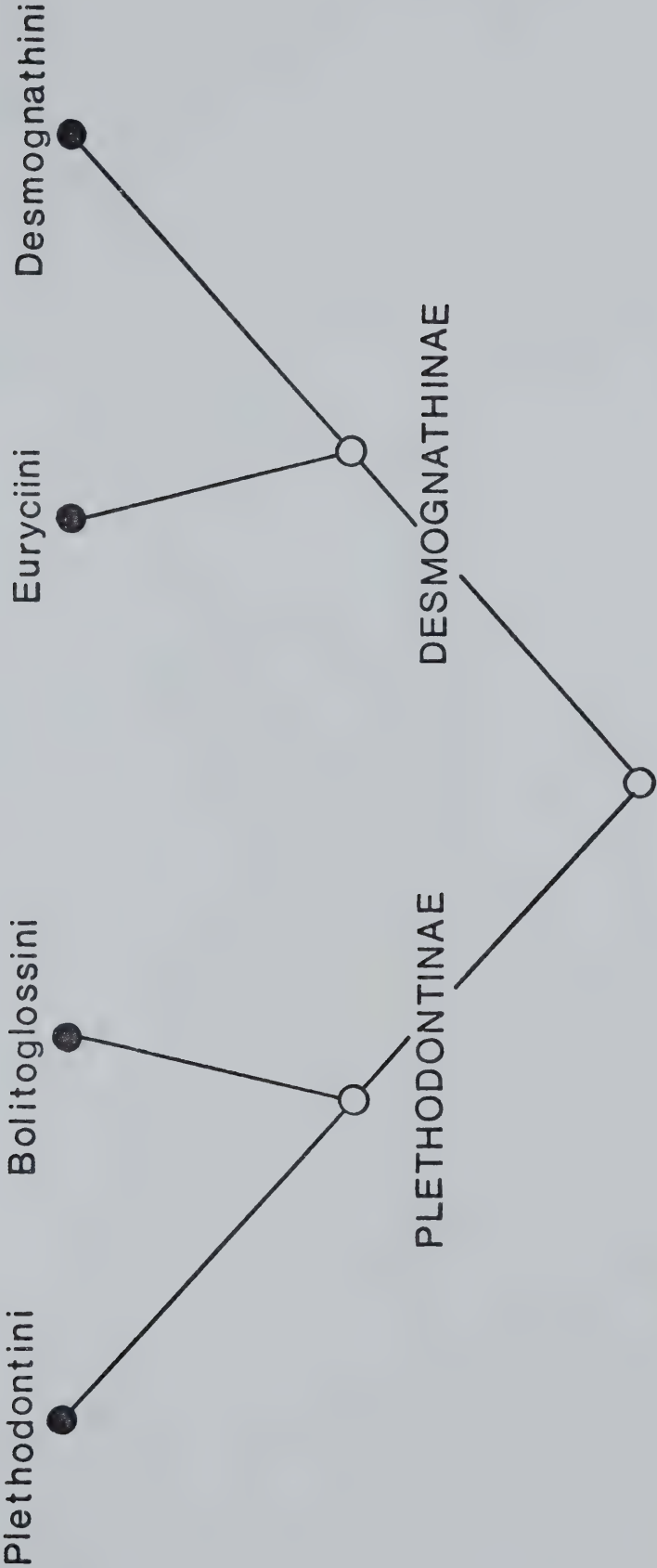


Figure 101. Proposed cladistic relationships within the family Salamandridae; generic groups are defined in the text and in Table 3; see text for discussion.

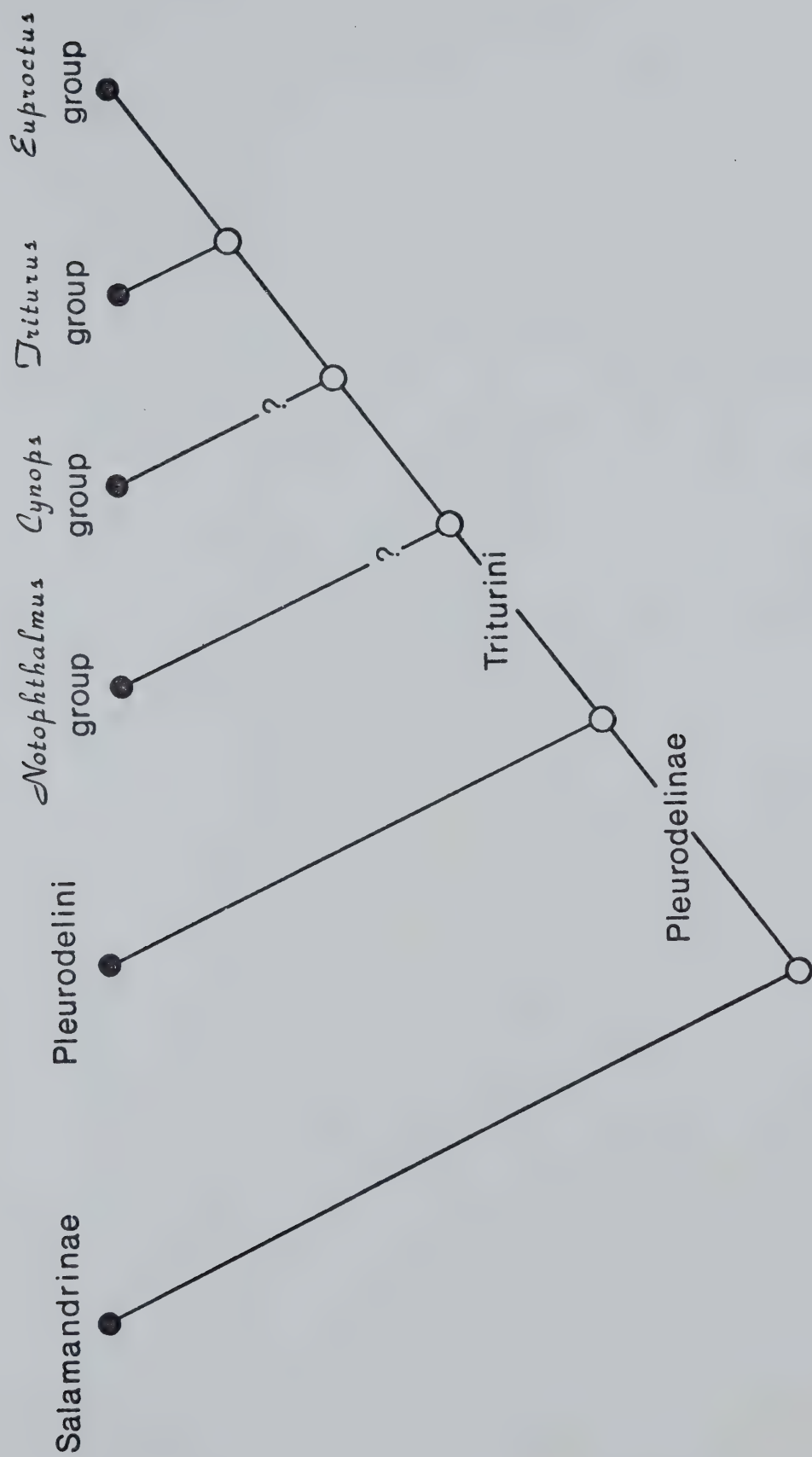


Figure 102. Proposed cladistic relationships for the suborder
Archaeocaudata; see text for discussion.

Figure 103. Proposed cladistic relationships for the suborder
Neocaudata; see text for discussion.

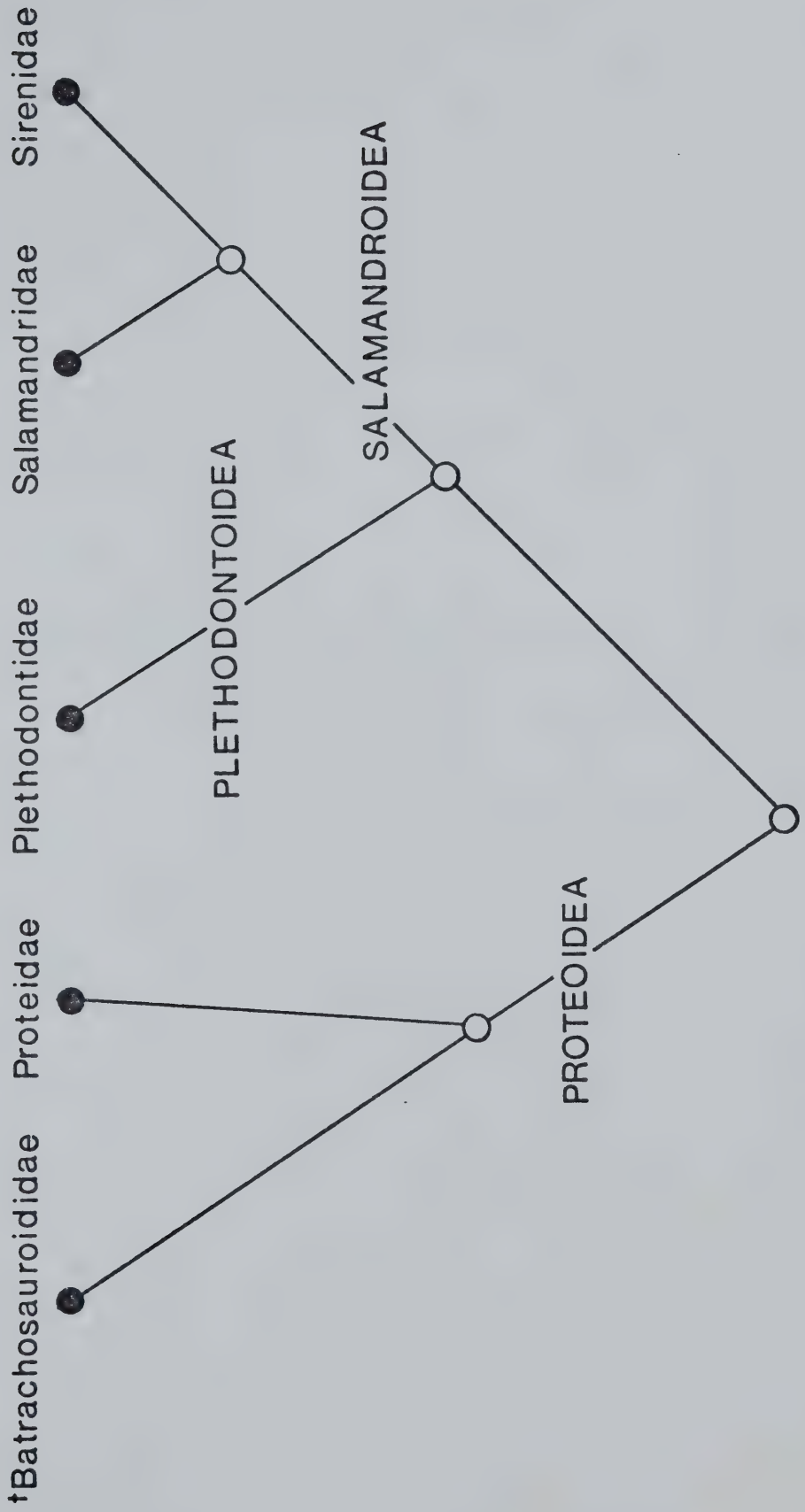


Figure 104. Phylogenetic reconstruction proposed for the order
Caudata; see text for discussion.

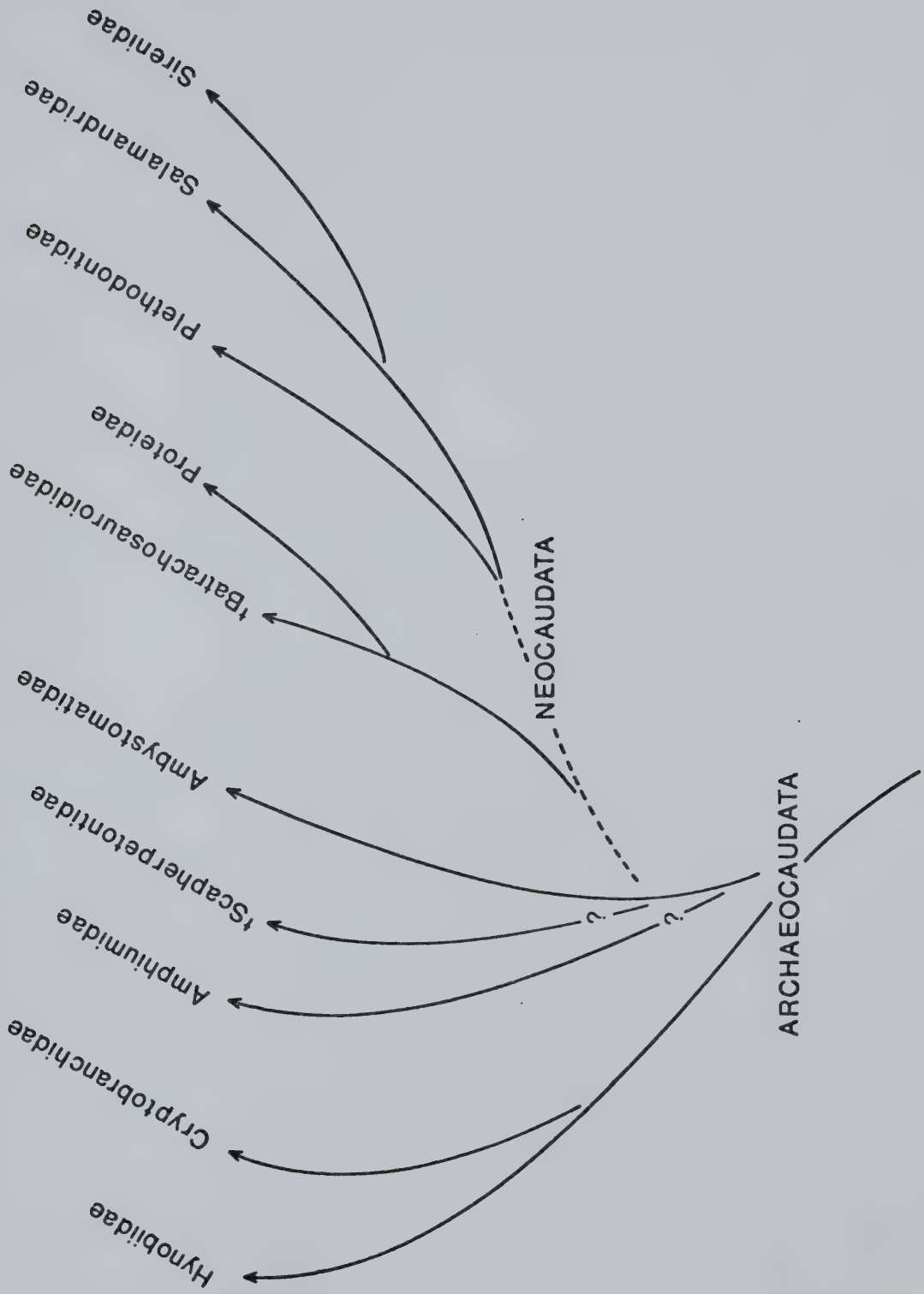
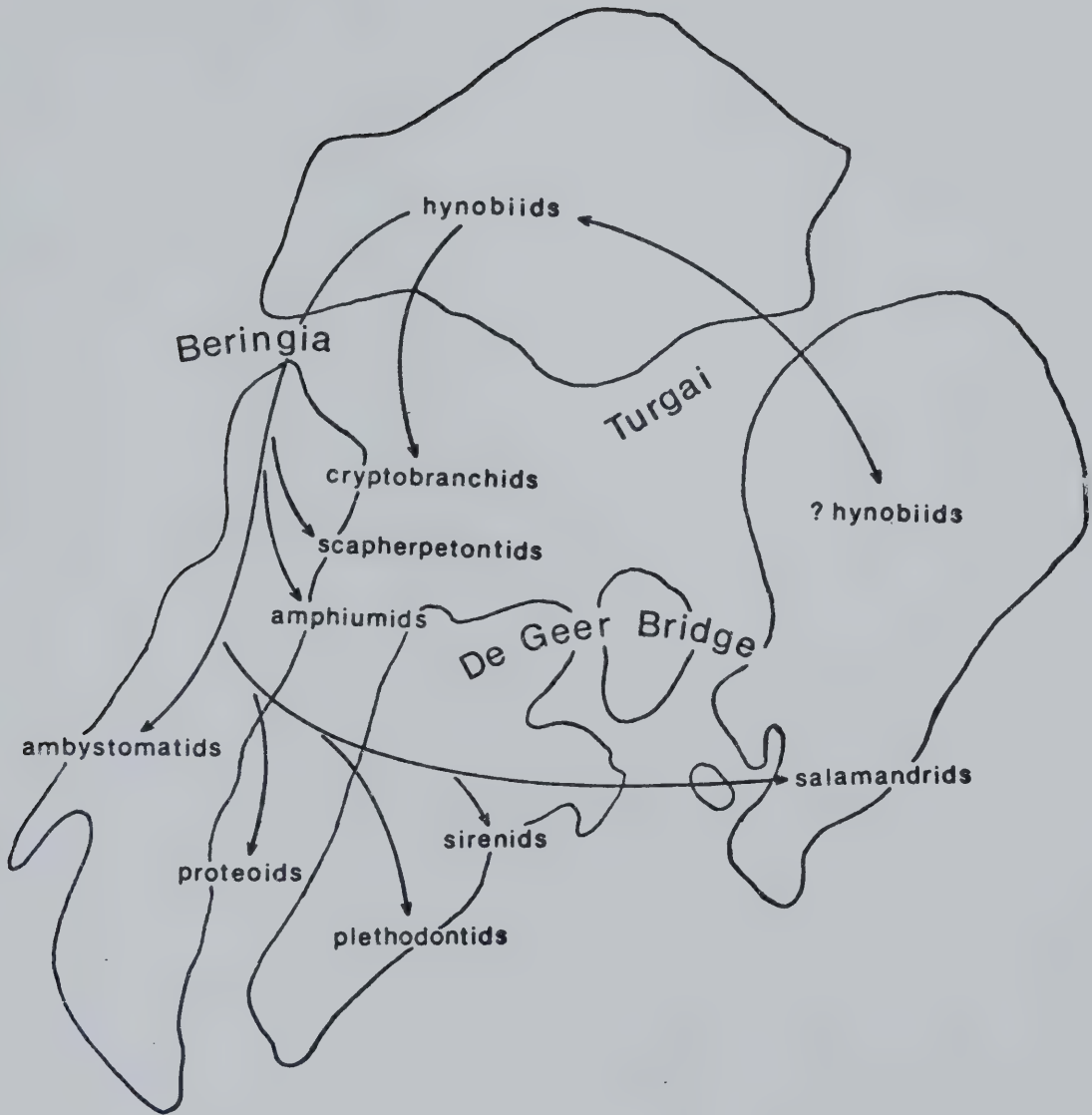


Figure 105. Tentative dispersal patterns within the order Caudata, shown on a polar sketch of the northern hemisphere in Late Cretaceous time; see text for discussion.



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